

Establishment of woody plants in mediterranean old fields: opportunity in space and time

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Abstract

The establishment of woody plants following agricultural abandonment in the Mediterranean region is a very widespread process which underlines the extent of the rural exodus. The installation windows in space and time were studied in the French Mediterranean region for two common woody plants, *Buxus sempervirens* and *Fraxinus angustifolia* and for a group of common woody fleshy-fruited species. These plants differ in their principal modes of dispersal which are respectively, barochory, anemochory and ornithochory. Their installation was analyzed in relation to the seed shadows, the spatial patterns and the age structures of the seedlings. The majority of the seeds were dispersed over short distances, although some animal vectors may promote a limited amount of long distance dispersal. Hence, whatever the mode of dispersal, a few seeds are often dispersed far from the maternal plant. The combination of several dispersal types in one plant species is a frequently observed feature, one being dominant at a small scale, and related to successional processes, the other being dominant at a larger scale and related to invasive processes. In the old fields the spatial pattern of seedlings closely follow the observed seed shadows. However, competition with the maternal plants may lead to, in some cases, a recruitment deficit close to the seed-bearers. Age structures show that woody plants often install very early after the abandonment of cultivation and that the installation window in time is shortened by the development of a dense herbaceous cover. It is concluded that the installation of woody plants in Mediterranean old fields cannot be reduced to a general rule. The rate and extent of installation depends mainly on the spatial distribution of the seed-bearers, therefore of the spatial patterns of the landscape.

Introduction

Dispersal is a significant process of population, community, and landscape dynamics. Woody plant establishment is a physiognomically and functionally important stage of plant successions. The predictions of this installation in space and time had originated particularly stimulating hypotheses and models taking into account dispersal patterns.

Relationships between the spatial pattern of seedling recruitment and the seed shadow in woody

plants have been primarily studied in tropical trees (see Clark and Clark 1984). Janzen (1970) and Connell (1971) have explained the structure of tropical forests in relation to the non-coincidence of the seed shadow (maximum density of seeds close to the seed-bearer) and the spatial pattern of recruitment (maximum at a distance of the seed-bearer). They suggested that this discrepancy could be explained by a greater predation impact in the vicinity of the seed-bearer. Hubbell (1980) although in agreement with a significant role for predation, suggested that

survival, though very low close to the seed-bearer, may be sufficient to allow a certain degree of recruitment close to the maternal plant, due to the massive number of seeds dispersed here. Reviewing 24 data sets on tropical woody plants, Clark and Clark (1984) concluded that there is much evidence for progeny mortality, either density-dependent or distance-dependent, as suggested by Janzen and Connell, but they underlined that the causes of this mortality might be due to other factors than predation, such as intra-cohort competition or allelopathy. Hence generalizations cannot be made without carefully designed studies. Recently, Schupp *et al.* (1989) suggested that patterns of immigration, survival and recruitment of trees in different stages of tropical forests (categorized as recent gap, maturing gap and mature forest) closely depend on dispersal types (categorized as wind-dispersed, small-seeded animal-dispersed and large-seeded animal-dispersed).

In temperate regions, the subject has been less often tackled. Following the ideas of Clements (1916, 1936), studies on plant community dynamics frequently dealt with the interactions between vegetation and environment. It was commonly believed that only some plant species are able to colonize after a perturbation and that these early successional species modify the environment in such a way that it becomes more suitable for later successional species. As a result the importance of dispersal was diminished. The first critical papers against Clements' ideas (*e.g.* Gleason 1926, Egler 1954, Drury and Nisbet 1973, Connell and Slatyer 1977) mainly discussed the importance of ecological factors and were not directly concerned with dispersal. More recently, the role of dispersal in vegetation dynamics was explicitly, or implicitly, recognized following the emergence of a conceptual framework on patch dynamics (*e.g.* Pickett and White 1985) and landscape ecology (*e.g.* Forman and Godron 1986).

In Mediterranean old fields, the dispersal process is one of the major driving forces during succession development. For instance, the frequency of different dispersal types regularly changes in time (Escarre 1979, Escarre *et al.* 1983, Lepart and Escarre 1983), and the formation and distribution of

patches of fleshy-fruited plants originate in the behaviour of the birds which disperse their seeds (Debussche *et al.* 1982, 1985). It was also shown that trees, according to their dispersal type and other life-history traits, may have narrow invasion windows (*sensu* Johnstone 1986) in space and time, and that they may install in old fields immediately after abandonment following cultivation, or even during cultivation (Acherar 1981, Acherar *et al.* 1984, Escarre 1979, Escarre *et al.* 1983, Debussche *et al.* 1982).

The aim of this paper is twofold. 1) To compare the invasion windows, in space and time, of common woody plants in Mediterranean old field successions, based on their seed shadows, the spatial patterns of their seedlings and the age structures of their populations. 2) To discuss these data sets in relation to existing hypotheses and models.

Study area and studied plants

The study area (ca 43°40' N, 03°40' E) is located in the Languedoc region of southern France, between the Massif Central and the Mediterranean sea, to the north of Montpellier. The climate is sub-humid to humid mediterranean with cool to cold winters (see Daget 1977). Most of the area's substrate is limestone. In this area, the landscape is diversified with a mosaic of old fields abandoned at different periods that permits an indirect reconstitution of post-agricultural successions (see Escarre 1979, Escarre *et al.* 1983).

The studied woody plants are: 1) *Buxus sempervirens* L., a shrub or small tree, whose seeds are mostly barochorous, 2) *Fraxinus angustifolia* Vahl, a tree, whose winged seeds are wind-dispersed, 3) a group of species with fleshy fruits, dispersed by vertebrates (birds and mammals).

Buxus sempervirens is an up to 5 m evergreen monoecious shrub or small tree widely distributed in Portugal, Spain, France, Italy, Balkans, Asia minor, Algeria, with scattered populations in Morocco and northwards in Ireland (Timbal 1975). It is a very widespread plant in the Montpellier region, especially in the garrigue and oak coppices. It flowers in early spring, producing a fruit 7 mm

long comprising a capsule with 6 seeds, each ca. 5 mm long. In the study region dispersal occurs in summer and is essentially barochorous, but water dispersal and myrmecochory may also occur (see Briquet 1912). Seeds germinate in April (Koechlin 1980).

Fraxinus angustifolia is an up to 20 m deciduous tree distributed over Portugal, Spain, Southern France, Italy, South-Central Europe, Balkans, North Africa and Asia minor (Timbal 1975). In the Montpellier region it is a common tree in moist woodlands, along rivulets and ditches, and on river banks. Flowering takes place at the end of winter. The fruit is a 25–45 mm long samara with a lanceolate wing. In the study region, dispersal by wind occurs from the end of summer into autumn and winter (Lepart and Debussche unpublished). Water dispersal seems to occur frequently as observed for other *Fraxinus* species (e.g. Thébaud and Debussche 1990).

Fleshy-fruited plants constitute a group of herbs, vines, shrubs and trees in the study area, with 65 native taxa known in the Montpellier region, two thirds of which are woody (Debussche *et al.* 1987, Debussche 1988). Their seeds are mostly bird-dispersed, although mammal dispersal has also been observed (Debussche and Isenmann 1989). Widespread in clear coppices, at forest edges, in garrigues, on rocky outcrops, many of these plants (e.g., *Cornus* spp., *Juniperus* spp., *Phillyrea* spp., *Pistacia* spp., *Prunus* spp., *Rhamnus* spp.) frequently invade abandoned vineyards and orchards (Debussche *et al.* 1982, 1985) and extensive rangelands (Strasberg 1987).

Methods

The installation of *Buxus sempervirens* in old fields was studied by Koechlin (1980), 25 km northwest of Montpellier. Dispersal distance was measured in August by sifting and hand-picking the seeds from the litter along a transect beginning at the trunk of a seed-bearer. The spatial pattern of installation was determined by mapping seedlings in June, when seedling survival still remained 100% after germination. At this time, the height of each in-

dividual was estimated. The mapped area encompassed a large stone pile which had been a refuge for woody plants when the land was under cultivation. Age structure was determined by counting the rings on stem sections.

The installation of *Fraxinus angustifolia* was studied by Lepart and Debussche (unpublished) in old fields, 2 km north of Montpellier. These old fields were bordered on one side by a hedge of *F. angustifolia*. Dispersal distance was measured from August to April, by collecting seeds in a transect of seed traps leading from the base of the maternal tree towards the old field. The spatial pattern of establishment was described by mapping the seedlings in areas of old fields neighbouring the hedges. Age structure was determined by counting the rings on stem sections.

The installation of fleshy-fruited plants was studied by Debussche *et al.* (1982, 1985), Koechlin and Debussche (unpublished), Debussche and Isenmann (unpublished), in old fields, orchards and patchy habitats of coppices and garrigues in several localities of the study area. Dispersal distances from the maternal plants and seed shadows were measured by collecting seeds in seed traps arranged in different designs according to the type of vegetation monitored. The spatial pattern of establishment were determined by mapping the seedlings in relation to hedges containing seed-bearers and perching sites. Age structure were determined by counting the rings on stem sections.

Results

Buxus sempervirens

Dispersal is a short-distance process for the great majority of the seeds of this species (Fig. 1). The maximum density of seeds was found 0.4–0.6 m from the trunk of the maternal plant, *i.e.*, at the edge of the crown shadow where the greatest number of capsules are located. No seed was found further than 2.8 m from the parent.

125 years after abandonment from cultivation, the colonization of the species, from the stone pile outwards in the old field, remained low and has es-

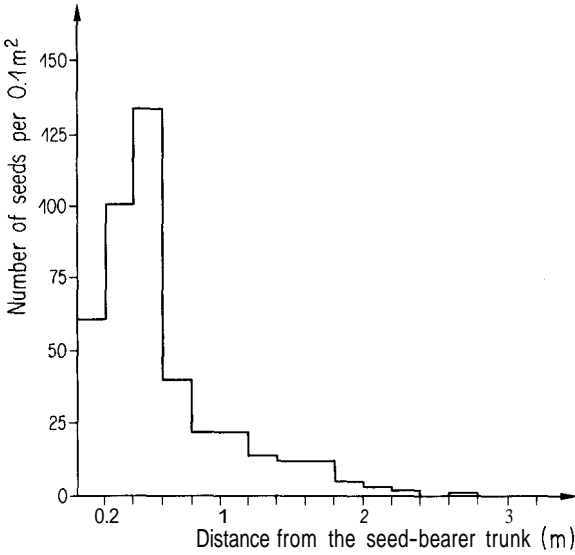


Fig. 1. Relationship between seed density contained in the upper soil layer and distance from the trunk of a 1.6 m and 50 year old *Buxus sempervirens* (after Koechlin 1980).

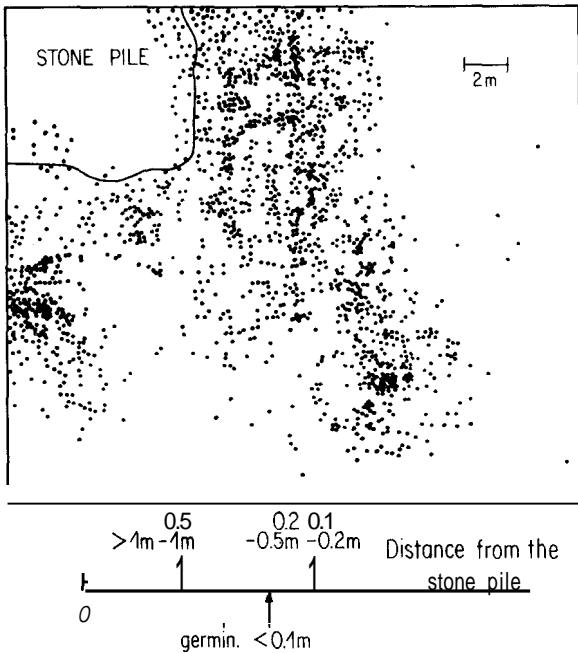


Fig. 2. Installation of *Buxus sempervirens* in a 125 year abandoned old field (after Koechlin 1980). Top: map showing the distribution of *Buxus sempervirens* ($n = 1588$ individuals) which has spread from the stone pile refuge towards the old field. Bottom: distance from the stone pile of the barycentres of 6 shrub height classes; the adopted scale is the same as for the map.

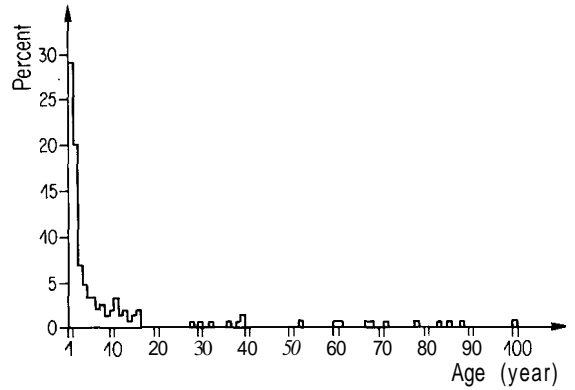


Fig. 3. Age structure of the *Buxus sempervirens* population installed in a 125 year abandoned old field ($n = 144$ individuals sampled along a transect from the stone pile towards the old field) (after Koechlin 1980).

essentially involved an 8 m-wide ring around the stone pile plus a 6×8 m extension in the stone pile corner direction (Fig. 2). This spread is illustrated by the order of the height barycentres: the tallest (and oldest) shrubs were found on, or close to, the stone pile, whereas plant height decreased with distance (Fig. 2), although seedlings (< 0.1 m tall) were not consistent with this gradient. Several factors may influence this distribution pattern (Koechlin 1980): 1) the short-distance dispersal which concentrates seedlings close to the maternal plant, 2) the high stone cover adjacent to the stone pile which prevents the seeds from germinating, 3) the 100% mortality of progeny under the dense canopy of the oldest seed-bearers.

The age structure diagram shows an inverse-J shape (Fig. 3). During the 16 years preceding the study recruitment occurred but in the 11 year-period leading up to the study seedling survival was 0%. There is no evidence of installation during the 25 years period after abandonment.

Fraxinus angustifolia

During the monitored dispersal period (August–April) the majority of seeds were dispersed either just under or up to a few metres from the maternal tree (Fig. 4). Though several windy days occurred during this period, the decrease of seed density with

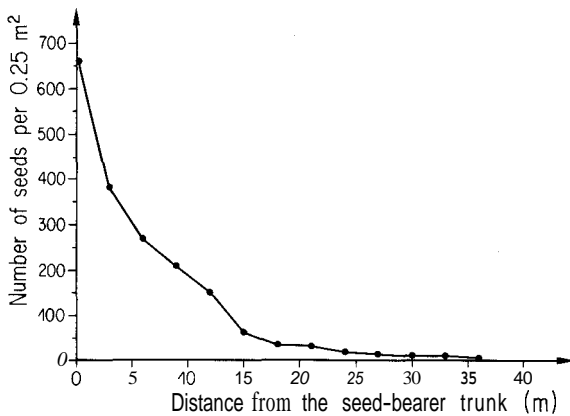


Fig. 4. Changes in the density of seeds of *Fraxinus angustifolia* collected in seed-traps with the distance from a 12–14 metre high hedge of seed-bearers (after Lepart and Debussche unpublished).

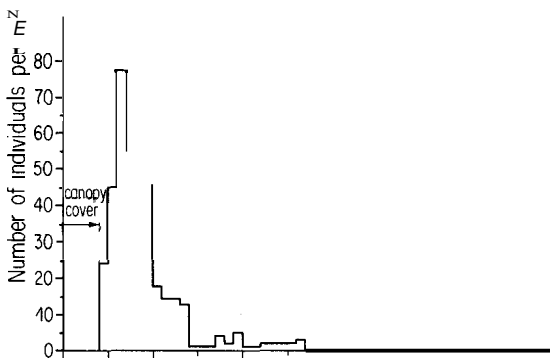


Fig. 5. Changes in the density of *Fraxinus angustifolia* seedlings in an abandoned 11 years old field with the distance from a 12–14 metre high hedge of seed-bearers; census made in November when all the germinations had perished (after Lepart and Debussche unpublished).

distance was rapid (negative exponential shape) and a small number of seeds, 7, 8 and 3 were respectively collected at a distance of 30, 33 and 36 metres from the trunk of the seed-bearer.

Just 11 years after abandonment from cultivation at the vineyard, the spread of the species had become rather dramatic (Fig. 5). No individual was censused under the canopy cover. The densest installation took place in the 4–14 m distance zone with very high densities up to 78 seedlings per m². The density remained constant and much lower (0–5 seedlings per m²) throughout the 14–36 m

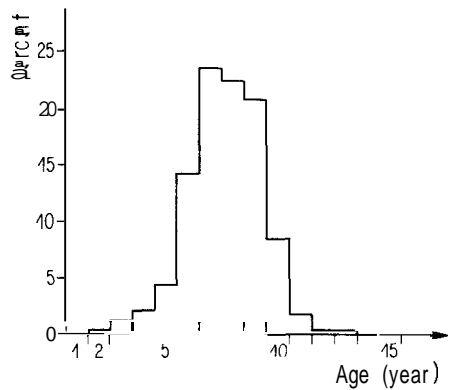


Fig. 6. Age structure of the *Fraxinus angustifolia* seedling population installed in a 11 year abandoned old field; census made in November when all the germinations had perished ($n = 374$ individuals sampled along a transect from the hedge towards the old field) (after Lepart and Debussche unpublished).

distance zone. Only scattered individuals were observed at greater distances.

The age structure diagram clearly shows that the recruitment rate had been decreasing for several years and that seedling survival was zero in the year of observation (Fig. 6). It is noticeable that a few seedlings installed before the definitive abandonment due to the fact that the maintenance of such vineyards is usually less and less efficient during the years leading up to abandonment.

Fleshy-fruited plants

Previous studies on the dispersal of fleshy-fruited plants in southern France (Debussche *et al.* 1982, 1985; Debussche and Isenmann 1985, 1989) and in North-American old fields (McDonnell and Stiles 1983 and McDonnell 1986) provide evidence for three types of seed shadow, according to the dispersal vector (Fig. 7).

Small-sized birds ('type a') generally consume small-sized fruits, the seeds of which are dispersed according to two density patterns: 1) a negative exponential decrease over a distance of up to 50 metres, 2) localized increases under pioneer shrubs or trees used as perching places. Seed densities may rise up to a few thousands per m² and per year. The more the old field is invaded by patches of shrubs and trees the greater the seed dispersal distance.

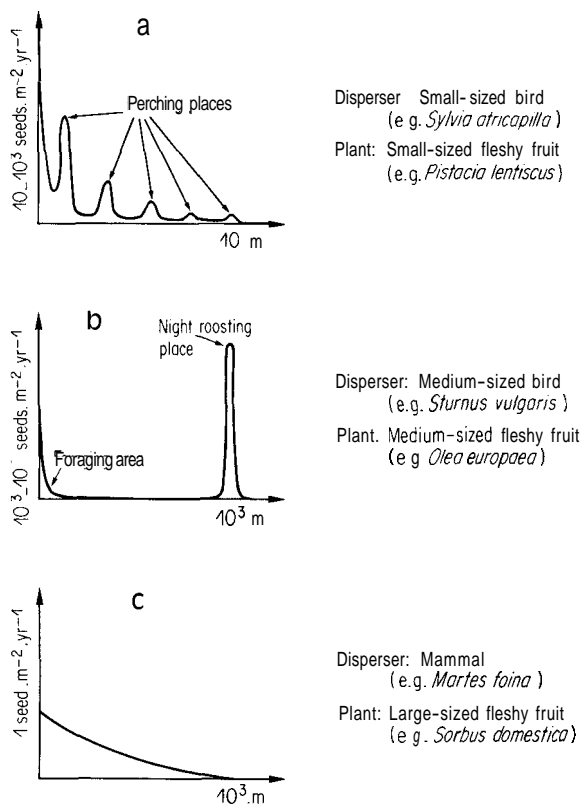


Fig. 7. Three types of seed shadow generated by vertebrate seed dispersers in the Mediterranean region (adapted from Debussche *et al.* 1982, 1985, Debussche and Isenmann 1985, 1989 and unpublished data; see also McDonnell and Stiles 1983).

Medium-sized birds ('type b') consume on average larger fruits than smaller birds. They are represented in the study region by species (*e.g.* *Sturnus vulgaris*, *Turdus sp. pl.*) which, during their wintering stay, roost in small or huge bands in sites up to several kilometres from the foraging area. These roosting places may be chosen in the hedges bordering old fields or in dense clumps of pioneer trees in old fields. Huge amounts of seeds may be deposited under the roosting places. It is assumed that the seed shadow in old fields throughout the foraging area is similar to 'type a' described above.

Mammals ('type c') often consume large fruits, the seeds of which are dispersed over a territory of tens or a few hundreds of hectares. Only old fields yet fairly invaded by shrubs and trees seem to be concerned by this dispersal. At a large scale, seed

density remains low. However, as some mammal species, such as the European badger (*Meles meles*), regularly lay their scats at very restricted spots over their territory (see *e.g.*, Mouchès 1981) a strong increase in seed density exist in such sites.

After 61 years of abandonment, an olive grove studied by Koechlin and Debussche (unpublished), showed a spatial pattern of seedlings installation which closely fits the 'type a' seed shadow model (Fig. 8). The maximum seedling density was obviously associated with the presence of olive trees, which are used as perching places for dispersers. Simultaneously, there was a decrease in the density of seedlings from the edge of the coppice which was rich in fleshy-fruited plants towards the edge of the coppice poor in fleshy-fruited plants.

The major woody plants which invaded three orchards studied by Debussche *et al.* (1982) presented different types of age structure (Fig. 9). It was observed in each of these cases that installation had taken place very soon (1–3 years) after the abandonment of cultivation, or even a few years (up to 4 years) before it, when the upkeep of the orchard would have been less careful. For two species (*Eunonymus europaeus* L. and *Cornus sanguinea* L.), the installation of the seedlings was still continuing, whereas in three others (*Pistacia lentiscus* L., *P. terebinthus* L. and *Phillyrea angustifolia* L.) the installation rate was decreasing strongly.

Discussion and conclusion

Seed shadow

For most of the studied plants the **bulk** of seeds were dispersed over a few metres or tens of metres from the maternal plant. However, dispersal by vertebrates was determined by the behaviour of the dispersers and many seeds were deposited much further from the seed-bearer (> 100m) when mammals and some bird species were the dispersal agents. Short distance seed dispersal (from some metres to some tens of metres) is the rule for the great majority of herbaceous plants and shrubs (*e.g.* Sheldon and Burrows 1973; Friedman and Orshan 1975; Harper 1977; Stamp and Lucas 1983;

Abandoned olive grove

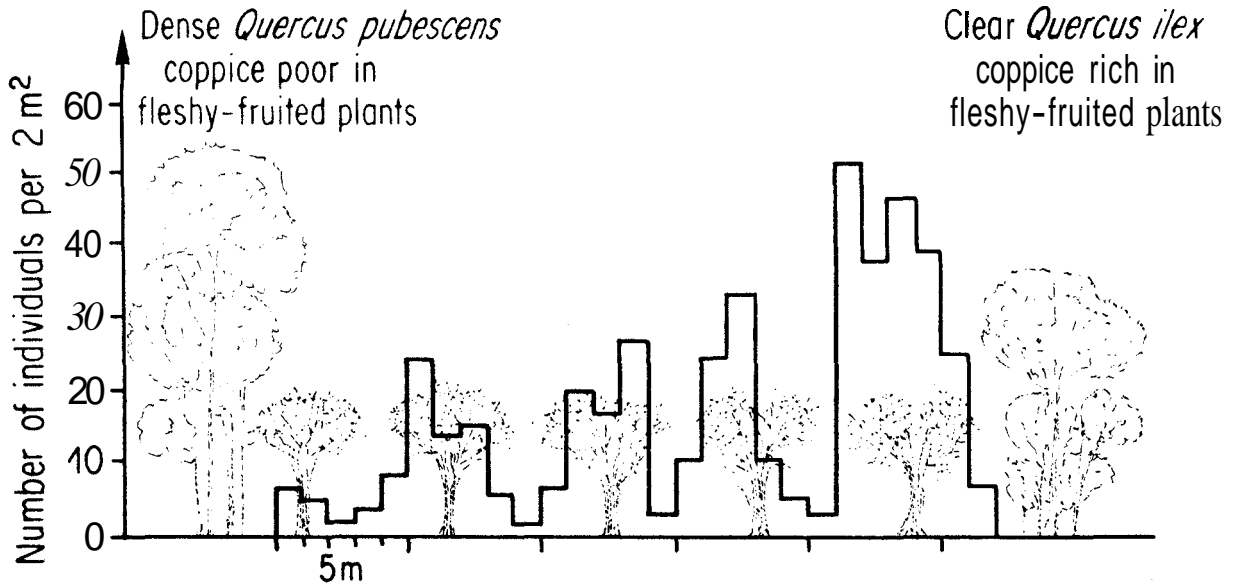


Fig. 8. Changes in the density of seedlings of fleshy-fruited woody plants ($n = 10$ species) in a 61 year abandoned olive grove surrounded by oak coppices along a cross section encompassing the olive trees (after Koechlin and Debussche unpublished).

Troumbis and Trabaud 1986; McEvoy and Cox 1987), and wind-dispersed trees (Harper 1977; Augspurger 1983; Acherar *et al.* 1984; Guries and Nordheim 1984; Lamont 1985; Johnson 1988). Long distance dispersal (a few kilometres) by vertebrates is well-known for the birds which collected and hide seeds, such as *Garrulus glandarius* with acorns (Bossema 1979) and *Nucifraga columbiana* with wingless seeds of *Pinus edulis* (Vander Wall and Balda 1977; Tomback 1982; Tomback and Linhard 1990). However small rodents, which store seeds (beechnuts, acorns, ...) in caches, move these seeds only a few metres (Jensen 1985).

Even in the case of a short distance dispersal vector there is usually a small number of seeds which are dispersed great distances from the seed-bearer. This phenomenon is particularly dramatic when observed as the installation of new species on islands or by the presence of isolated individuals very far from the distribution area of the plant (*e.g.* Ridley 1930; Docters van Leeuwen 1936).

To associate a particular dispersal type with a particular plant species is useful, but is very often an over-simplification. Generally, plant species

may have their seeds dispersed in several manners, one of these being predominant, or easier to detect. *Prima facie*, some dispersal agents may not appear to be important because they are not evidenced by adaptative structures of the seed (see Erikson *et al.* 1983). However, these agents may often be very efficient depending on site conditions. It was also frequently observed that several dispersing agents may act consecutively to disperse individual seeds (*e.g.* Roberts and Heithaus 1986; Gonzalez-Espinoza and Quintana-Ascencio 1986). We have suggested elsewhere (Lepart and Debussche 1991) that, for a given plant, one dispersing agent may be effective for short distances and can be associated with successional processes, whereas, for the same plant, another dispersing agent may be effective for long distances and can be associated with invasion processes.

In the case of *Buxus sempervirens* a small-scale survey of dispersal was made which fits with successional processes. At a larger scale, water may perform long distance dispersal of this plant along eroded slopes and on the banks of summer dried-up streams (see Troumbis and Trabaud 1986 for *Cistus*

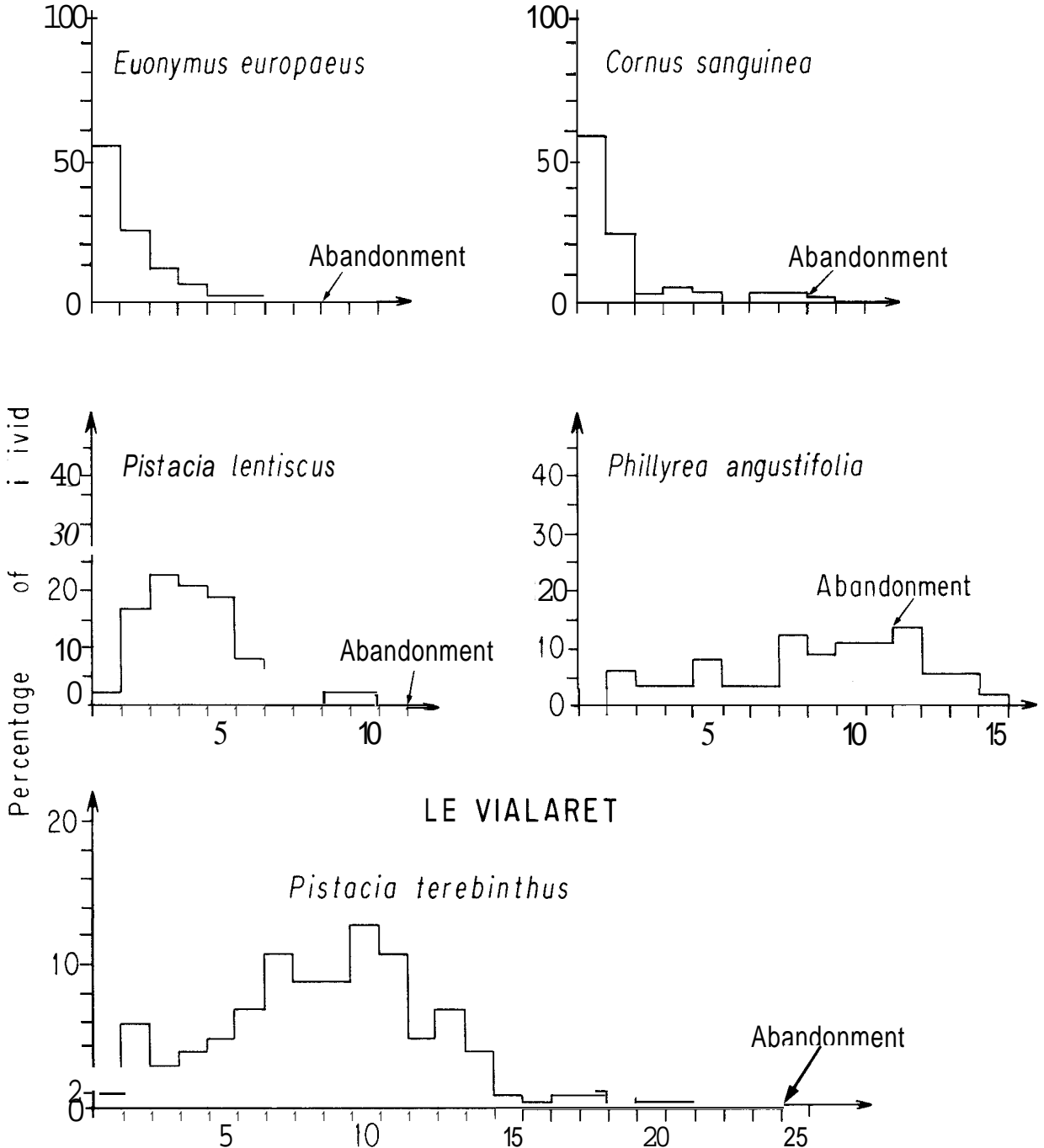
S^t MARTIN DE LONDRES

Fig. 9. Age structure of 5 fleshy-fruited woody plants installed in orchards at 3 localities (in Debussche *et al.* 1982).

dispersal. *Fraxinus angustifolia* was studied at the same scale and it is also water which allows this tree to spread for kilometres along riversides, thanks to

the buoyancy of the winged seed (see Thébaud and Debussche 1990 for details of *F. ornus* dispersal). Each fleshy-fruited plant is dispersed by several

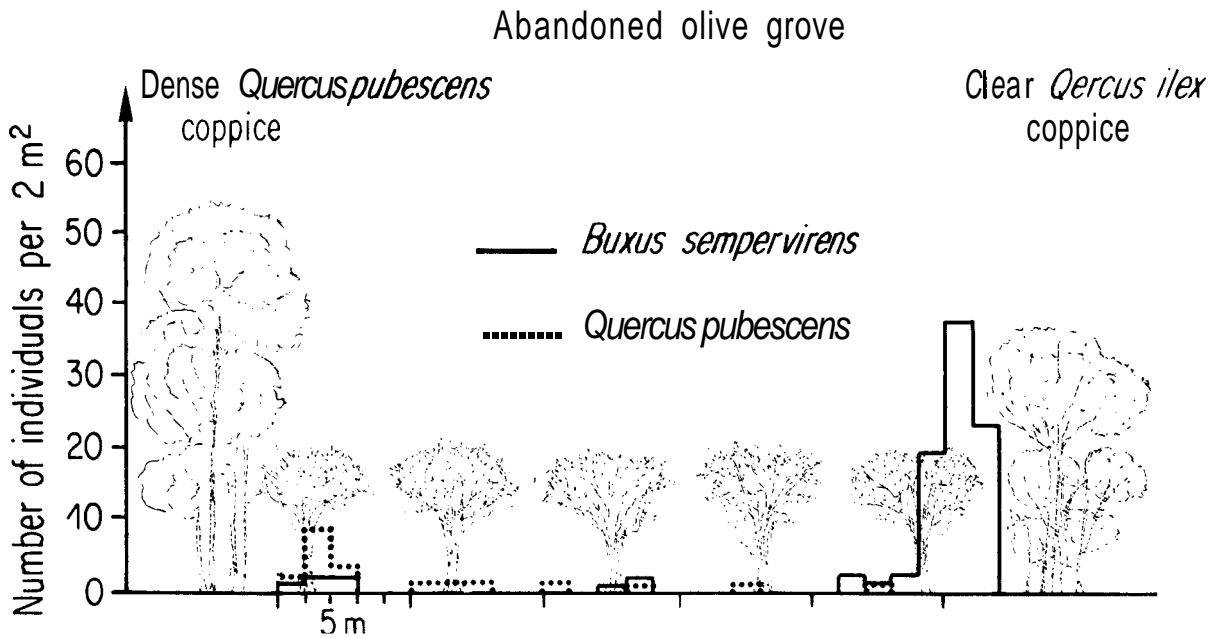


Fig. 10. Changes in the density of seedlings of *Buxus sempervirens* and *Quercus pubescens* in a 61 year abandoned olive grove surrounded by oak coppices along a cross section encompassing the olive trees (after Koechlin and Debussche unpublished).

vertebrate species which may be birds and mammals of different sizes, behaviours and habitat preferences (Debussche and Isenmann 1990). Therefore a plant may present a mixture of different types of seed shadow. The seeds of these plants may also be washed away along slopes or deposited by floods on streambanks, many kilometers downstream from the place to which they were dispersed by animal agents. Water dispersal is probably, at a large scale, an important dispersing agent for many plants (see *e.g.* Koutstaal *et al.* 1987), as has been well-illustrated by the rapid spread of several tree species following the retreat of the ice-sheet after the last glaciation (see Huntley and Birks 1983).

The spatial pattern of seedlings

The spatial pattern of seedlings was closely related to the observed seed shadows. There was one dominant local dispersing agent in each studied old field, which determined the spatial pattern of recruitment. However, in some sites, the spatial distribution of seedlings showed that several agents were involved in the dispersal of a single species

(Fig. 10). In the olive grove described in Fig. 8 two dispersing agents might have existed for *Buxus sempervirens* and *Quercus pubescens* Willd. Barochory explains the location of the seedlings of both species nearby the stone wall surrounding the olive grove but not the isolated seedlings at a distance. Dispersal by ants may explain the isolated seedlings of *Buxus sempervirens* and the observed unconsumed acorns of a small rodent cache provides an explanation of the isolated seedlings of *Quercus pubescens* (Koechlin and Debussche unpublished). The spatial uniformity of ecological conditions due to cultivation is such that, when cultivation has stopped, recruitment can more easily coincide with the seed shadow (see Johnson 1988).

Fraxinus angustifolia showed a conspicuous difference between seed and seedlings density close to the maternal plants, there being a deficit of seedlings in the vicinity of the seed-bearer. The dense canopy cover and the bending of the stems of surviving seedlings suggest a strong shading effect of the maternal plant (Lepart and Debussche unpublished). The early falling of the leaves of numerous seedlings in summer suggests that intense competition for water occurs between seedlings (Lepart and

Debussche unpublished). The observed pattern is broadly consistent with Janzen and Connell's model, but with two main differences: 1) predation appears to be a non-significant cause of the observed recruitment deficit, 2) distance between the seed-bearer and the offsprings is small. This last point will result in the formation of a close and dense stand of trees as is frequently observed in the study region, not the large spacing of the trees as observed in tropical forests (e.g. Howe *et al.* 1985; Dirzo and Dominguez 1986). Very similar relationships between the seed shadow and the spatial pattern of seedlings are observed in Mediterranean old fields colonized by *Pinus halepensis* (Acherar 1981; Acherar *et al.* 1984).

Age structure

Some studied species showed age structures with an inverse-J shape (e.g. *Buxus sempervirens*) whereas others had few or no individuals in the younger classes (e.g. *Fraxinus angustifolia*). Furthermore, woody individuals often installed before abandonment. Although the studied species do not have a long lasting dormant seed bank, the seeds of *Fraxinus angustifolia* are probably dormant for one year, as observed for *F. excelsior* L. (Villiers and Wareing 1960). The seeds of *Phillyrea angustifolia* can also germinate one year after dispersal if they have not encountered previously sufficiently moist conditions in the soil (Lepart pers. obs.).

The interpretation of age structures, because it makes a number of assumptions concerning past processes and events must be made cautiously (Harper 1977). Past events such as severe droughts and frosts, fires, pest invasions, human impacts, are not always detectable and correctly identified. In old fields, these events interfere with the successional processes linked with competitive, edaphic and microclimatic changes.

In the case of *Buxus sempervirens*, Koechlin (1980) explained alternation of phases of recruitment and non-recruitment by occasional changes in anthropic actions on the field, as frequently observed in the study region. A low grazing pressure and a fairly dense cover of shrubs and trees might

have favoured the installation success, whereas overgrazing, sometimes accompanied by tree cutting, might have totally or partially prevented recruitment. Koechlin (1980) underlined that during their first summer the young seedlings had poor survival in the close vicinity of the seed-bearers and in full light. Maximum survival was realized under intermediate conditions.

The invasion window of *Fraxinus angustifolia* is restricted in time. As no perturbation has occurred since the vineyard was abandoned, the recruitment deficit can be linked to successional development. This deficit originated in the thick herbaceous cover of Graminae and Leguminosae which rapidly thrived in the years following abandonment (Lepart and Debussche unpublished). This thick herbaceous cover reduces germination success and seedling survival due to competition for water and light; a frequently observed process when trees invade dense grasslands (e.g., van Auken and Bush 1988; Brown and Archer 1989).

Some fleshy-fruited plants showed age structures with an inverse-J shape, others showed age structures similar to *Fraxinus angustifolia*, with rather narrow invasion windows. For all species initial colonisation occurred during a short period just before or after abandonment. Since the studied old fields did not experience perturbations after cultivation abandonment the decrease in recruitment can be interpreted in the same manner as that for *Fraxinus angustifolia*.

Connell and Slatyer (1977) proposed three models to represent the changes in vegetation composition during successional development: facilitation, tolerance and inhibition. The facilitation model hypothesises that some species can only establish if pioneer species have previously modified and prepared the habitat; under the tolerance model there is independence between the pioneer species and the following species; finally, the inhibition model implies that some species prevent other species from establishing and are only replaced when they die or as a result of disturbance. The existence of these three different models along successional development is a general trend of the Mediterranean old fields succession in the study region (Escarre 1979; Escarre *et al.* 1983). Our

results show that: 1) the tolerance model applies as long as there is a close fit between the seed rain and the pattern of installation of the seedlings, 2) for some of the fleshy-fruited plants, and for *Fraxinus angustifolia*, the inhibition model fits with the non-recruitment period, 3) the facilitation model appears to describe the installation of *Buxus sempervirens*, and, in a different way, the installation of fleshy-fruited plants under pioneer shrubs and trees. This changing importance of the different models during successions seems to be a general rule (Walker and Chapin 1987; Connell *et al.* 1987).

Nevertheless, installation of woody plants in Mediterranean old fields involves complex processes which cannot be reduced to a general rule. Invasion windows in time are open for many woody plants much earlier during succession development than it is generally believed. Invasion windows in space are largely limited by the dispersal ability of seed-bearers. It is thus crucially important to determine the spatial arrangement of the landscape if changes of vegetation pattern are to be understood and made predictable.

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