

Dynamics of Mediterranean vegetation following clearing and herbicide treatments in newly planted forests

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Abstract

The responses of the natural vegetation after clearing and herbicide applications commonly used to facilitate establishment of newly planted coniferous forests, were studied in the Judean Mountains, Israel. Two experimental sites were selected. In each site, 45 quadrats of 12 x 12 m were marked and the existing vegetation was recorded. Total manual clearing of the aboveground vegetation was carried out and herbicide treatments, with different intensity and frequency, were applied. The results for both experimental sites showed that disturbance by clearing and herbicide applications produced drastic initial changes in community structure, diversity and species composition. However, subsequent spontaneous processes tended to restore to dominance the initially dominant species. Plant cover, species richness and diversity, were significantly reduced by herbicide treatments during the first two years. However, differences between treatments were no longer significant three and four years following the clearing and herbicide applications. A general trend toward successional convergence was observed, as quadrats of all treatments tended to return toward similar composition and structure. This convergence is explained by life history characteristics of the dominant species present at the sites.

Introduction

In agriculture and forestry studies, plant clearing and the use of herbicides, are commonly used as tools for management (Putwain & Harper, 1970; Viragh, 1987; Haywood, 1994; Aldrich & Kremer, 1997). Ecologists have long recognized the similarities between natural and some man-made disturbances (Bazzaz, 1983). Disturbance experiments have been used to examine patterns and to recognize key elements in the dynamics of plant communities (Pickett & White, 1985). The aim of some of these studies was to understand the effects of the disturbance agents on the dynamic of the vegetation, in order to provide management recommendations.

In Israel, disturbance of the natural vegetation by shrub clearing, burning, heavy grazing and browsing of domestic livestock, and by cultivation has been practiced since Neolithic times (Naveh, 1967, 1990). This period of time has probably allowed certain plant species to develop regeneration strategies, adapted to these common types of perturbations. In particular, the Batha community (dwarf shrubs, grasses and herbs associations) in

the Judean Mountains is considered to be adapted to the common types of disturbances (Litav *et al.*, 1962; Litav, 1969; Zohary, 1973). Therefore, plant removal of the aboveground structures by common perturbation agents would not be expected to considerably affect the structure of the Batha community. However, what would occur when a new or unpredictable agent, such as a non-selective herbicide, disturbs these communities? Would these plant communities change to a different composition and structure, or returned to one similar to that previous the disturbance?

This relates to the question of convergence/divergence in plant succession. Ecologists have long discussed whether secondary succession is a convergent or a divergent process (Van Hulst, 1978; Peet & Christensen, 1980; Inouye & Tilman, 1988; Leps & Rejmanek, 1991). In field studies, both convergence (Prach, 1985; Hattton & West, 1987) and divergence (Glenn-Lewin, 1980; Pineda *et al.*, 1981; Christensen & Peet, 1984), as well as mixed patterns (Rejmanek *et al.*, 1987; Inouye & Tilman, 1988; McLendon & Redente, 1990) have been reported. Several community aspects such as resource availability at the sites (Inouye *et al.*, 1987;

Inouye & Tilman, 1988; Carson & Pickett, 1990), niche widths of the dominant species at different stages (Christensen & Peet, 1984), initial colonization events (Glenn-Lewin, 1980; D'Angela *et al.*, 1988) and the previous history of the area (Facelli & Pickett, 1990; Myster & Pickett, 1990) may determine whether different sites converge or diverge.

The Jewish National Fund (J.N.F, the Forest Service in Israel) has been utilizing herbicides in the forests under its management, to facilitate establishment of newly planted coniferous seedlings. Casual observations indicated that clearing and the application of herbicides in the preparation of forest plantations drastically reduces biomass and diversity of the herbaceous vegetation in the first years. The subjective impressions created by the effect of the herbicides have caused several public confrontations between foresters and conservationists in Israel. However, no quantitative data was available on the magnitude of the effects of the herbicide applications on the plant communities. Further, the mechanisms and causes of variation in the short term of the Batha community, in response to clearing and herbicide applications, had been little studied. Indeed, few studies have considered successional pathways after disturbance in newly planted forests of Eastern-Mediterranean communities.

The aim of the present study was to analyze the changes in natural vegetation after disturbance by aboveground plant removal and herbicide applications in newly afforested areas in the Judean Mountains, and provide quantitative data to solve the public confrontation between foresters and conservationist in Israel.

The questions posed in this study are: 1) how is the structure and composition of the Batha plant community affected by pre-afforestation disturbances such as plant removal and herbicide applications? 2) Do the community responses to the initial disturbance result in convergent or divergent secondary successional pathways? 3) Is the dynamics of species in the post-disturbance period associated with life history attributes?

Materials and methods

The study areas

Two experimental sites were set up in newly forested areas in the Judean Mountains. The first site was

set up in September 1989, near Moshav Yishi (34° 58' E, 31° 50' N) located at an elevation of 220 m above sea level, on Rendzina soil on Eocene chalk (Soil names follow Dan *et al.*, 1970). The climate is Mediterranean, with a mean annual temperature of 19.8°C (Max. 24.9°C and Min. 14.7°C) and 493 mm annual rainfall falling mostly in winter (National Meteorological Service). The rainy season begins in October-November and ends in April-May. At least six months of dry weather characterize the region. Full meteorological data is available under request from the National Meteorological Service.

The second site was established a year later, in September 1990, near Moshav Matta (35° 03' E, 31° 43' N) located at an elevation of 620 m above sea level, on Terra Rossa soil on Cenoman hard limestone (Dan *et al.*, 1970). The climate is also Mediterranean, with a mean annual temperature of 17.5°C (Max. 22.4°C and Min. 12.7°C) and 537 annual rainfall (National Meteorological Service). Both areas were located on north-facing slopes. The two sites differed in biotic and abiotic characteristics, such as edaphic conditions, temperature and rainfall. However, a Batha-type plant community was developed in both areas, with differences in species composition.

Experimental design

The study was conducted in two areas of 0.7 ha, where 45 quadrats of 12 x 12 m were respectively marked. The pre-planting operations (clearing of the perennial vegetation) in Yishi and Matta site started respectively, in October 1989 and October 1990. The clearing of the aboveground biomass, was carried out in 36 quadrats, according to the common Jewish National Fund (J.N.F) practice (using shovels and hoes), while 9 quadrats remained uncleared. The herbicide used in the experiment was simazine (2-chloro-4,6-bis(ethylamino)-s-triazine). It is a soil-acting triazine herbicide with presumed non-selective effects (Ivens, 1989).

The quadrats were arranged in respect of a randomized block design with five treatments and nine blocks as replicates (Greig-Smith, 1983). The treatments were: A) Clearing + simazine treatment in autumn before planting, with standard dose (5 kg/ha) and again next autumn with the same dose (October 1989/1990 at the Yishi site and October 1990/1991 at the Matta site). B) Clearing + simazine treatment only before planting, with one standard dose (5 kg/ha). C) Clearing + simazine

treatment applying half of the standard dose (2.5 kg/ha) before planting and the remaining amount (2.5 kg/ha) in autumn of the next year. D) Clearing only, no simazine treatment. E) Control. No clearing, herbicide applications or planting operations.

Controls quadrats (E) could not be included within the blocks randomization since the area was planned as a forest and planting was not carried out on them. However, they were contiguous with the experimental area along its border, and included similar environmental heterogeneity.

The different herbicide doses were manually applied on the quadrats with a back sprayer. The herbicide was sprayed before the rainfall season started and remained 7 days on average on the soil surface, before being washed by the first rains.

The Yishi site was planted in November 1989 according to the common J.N.F practice, with six months old saplings of *Pinus brutia* Ten. The Matta site was planted in November 1990, with one-year old saplings of *Pinus pinea* L., *P. brutia* and *Cupressus sempervirens* L. Full details and results of tree establishment and growth are published elsewhere (Sternberg, 1994).

Sampling

Plant cover and composition were estimated by the interception point method (Mueller-Dombois and Ellenberg, 1974). Within the inner 10 x 10 m of each quadrat, ten fixed transects of ten meters lengths were placed at one meter distance between them. In each transect, every 20 cm a point was read, adding up to 50 points per transect, and a total of 500 points per quadrat. A point was read using a slender bar positioned exactly vertically to the ground. An outer belt 1 m wide within each quadrat was not sampled in order to remove direct edge effects. Vegetation was regularly recorded on 10-15, 14-19, 12-17 and 19-24 April in 1990 to 1994 respectively, during the peak season of primary production.

Species nomenclature follows Feinbrun-Dothan & Danin (1991).

Data analysis

Each observation in the analysis consisted of the mean of ten transects per quadrat. The relative cover of each species in a quadrat, was transformed by the arcsine square-root transformation (Sokal & Rohlf, 1995). Analyses of Variance (ANOVA) were

used to determinate differences among treatments. The analyses were carried out in respect to a randomized block design with five treatments and nine blocks as replicates. The Tukey HSD (honestly significant difference) test was used to compare differences of means among treatments for all pairs of combinations (SAS Institute Inc., 1990; Tukey, 1953). Species richness was estimated for each treatment by counting the total number of plant species intercepted in each quadrat and averaging over the nine replicates. Similarities in species composition among treatments was tested using Sorensen's similarity index (Greig-Smith, 1983). Species diversity was calculated from the cover values using the Shannon-Wiener index (Pielou, 1975). Differences in species diversity means, were tested with the T-test (Magurran, 1988).

A Raunkiaer's life forms analysis was done for all the survey seasons at both experimental sites. The analysis was based on the relative cover of each life form presented at each quadrat. ANOVA and Tukey HSD tests were used to analyze the data.

A classification of individual species into herbicide response groups was derived by considering the number of times a species was significantly ($p < 0.01$) more abundant in the areas where simazine was applied in site pairs. Three groups were recognized:

H+: Species in which significant differences in response to herbicide applications were usually due to higher abundance on the treated areas.

H-: Species in which significant differences in response to herbicide application were usually due to lower abundance on the treated areas.

Ho/Hx: Species which showed either no significant response, or a mixed response to herbicide applications, i.e., in some cases were significantly more abundant where simazine was applied and in other cases less abundant.

At the same time, using similar criteria, species were classified by their response to clearing. Three clearing response groups were recognized: C+, C-, and Co/Cx. Chi-square tests were carried out between the different response groups of both sites, in order to identify a distinctive trait that could unify these groups. Life forms of the species present in each group were considered in the analysis. Since the expected frequencies in some of the cells, were quite small, the chi-square distribution could not serve as a reliable approximation. Thus, computer simulations estimated the p values. Under the

assumption of independence between the response groups, 10000 random samples were drawn and the proportions of samples having a calculated chi-square were taken as an estimate for the unknown p values. Species with different responses to simazine (H+/H-) and clearing (C+/C-) were contrasted.

Results

Vegetation characteristics at the sites

During the study a total of 178 species were recorded at the Yishi site and 166 species at the Matta site. Relative plant cover in the control quadrats (treatment E) at the Yishi site was comprised by 46.8% of annual species and 53.2% by perennial species, mostly chamaephytes. At the Matta site, relative plant cover of annual species was 42.8%, while perennials cover was 51.2%. The undisturbed quadrats (control-treatment E), provided a reference of the floristic characteristics of the site previous to the clearing and herbicide operations and characterized the natural vegetation developing at the sites. Dominant species at the Yishi site were represented by dwarf shrubs such as *Sarcopoterium spinosum* (L.) Spach (ca. 28%) and *Majorana syriaca* (L.) Rafin. (ca. 10%), annual grasses such as *Avena sterilis* L. (ca. 11%), perennial grasses such as *Hypparhenia hirta* (L.) Stapf (ca. 8%) and annual legumes such as *Vicia palaestina* Boiss. and *Trifolium purpureum* Loisel. (ca. 5% and 4%, respectively). At the Matta site, dominant species included a tree and a shrub species (*Quercus calliprinos* Webb, ca. 6%, and *Pistacia lentiscus* L., ca. 5%, respectively), dwarf shrubs such as *S. spinosum* (ca. 24%) and *Cistus creticus* L. (ca. 9%), annual grasses such as *A. sterilis* (ca. 12%) and *Hordeum spontaneum* C. Koch (ca. 7%) and annual legumes such as *Trifolium stellatum* L. (ca. 5%).

Effects of treatments on species richness

Changes in species richness due to the herbicide and clearing treatments, are shown in Fig. 1. At the Yishi site (Fig. 1a), simazine applications significantly reduced species richness in quadrats where high doses were applied (treatments A and B) during the first and second year after planting ($F_{4,40} = 9.50$, $p < 0.001$ and $F_{4,40} = 11.50$, $p < 0.001$, respectively). The Tukey HSD test showed no significant differ-

ences among the cleared and uncleared controls and the low simazine dose treatment in the first year (D, E and C respectively). During the second year, cleared quadrats with no herbicide (D), showed significantly higher species richness than all remaining treatments. Quadrats with the highest herbicide doses (A), had significantly lower species richness than all other treatments. During the third and fourth year after planting, differences among the simazine treatments and the cleared and uncleared controls were small and not significant ($p > 0.05$).

At the Matta site a similar pattern was observed (Fig. 1b). Significant differences between treatments were noted during the first and second years ($F_{4,40} = 7.65$, $p < 0.0001$ and $F_{4,40} = 3.92$, $p < 0.01$, respectively). The 5kg/ha simazine treatments had

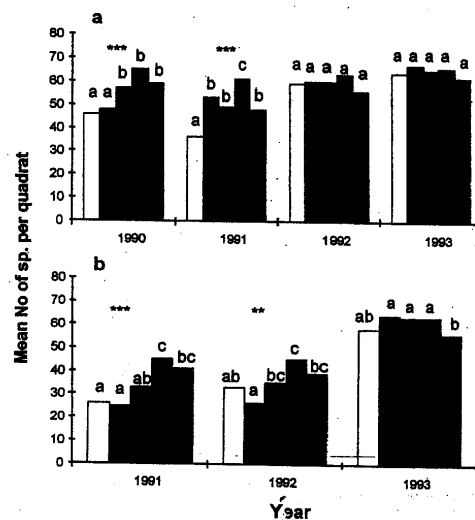


Fig. 1. The effects clearing and simazine treatments on species richness at (a) Yishi site and (b) Matta site. Treatments: A (□) Clearing + simazine treatment before and a year after planting (5 kg/ha); B (■) Clearing + simazine treatment only before planting (5 kg/ha); C (▒) Clearing + simazine treatment before and a year after planting (2.5 kg/ha); D (■) Clearing with simazine treatment omitted; E (■) Control (no clearing nor simazine treatments). Treatments were compared using one-way ANOVA and a subsequently HSD test. ** indicates $P < 0.01$, *** $P < 0.001$. Treatments bearing the same letter are not significantly different at $P < 0.05$.

fewer number of plant species during the first two years after planting, relative to cleared and uncleared controls. The clearing only treatment (D) had higher species richness than control, but differences were not significant. In the third year after disturbance operations, differences among simazine and cleared quadrats were small, and not significant ($p > 0.05$). However, they remained significantly higher than undisturbed quadrats.

Effects of treatments on floristic composition

Floristic composition lists between pairs of treatments were compared for both research areas during all survey seasons. High similarity indexes between treatments (Sorensen similarity index) were obtained for both sites (Table 1). Treatment E (control) is compared only with treatment D (clearing only) due to the type of disturbance. At

the Matta site, a general trend of increasing floristic similarity between treatments with time was observed (from 73.7% in 1991 to 95.5% in 1993), while at the Yishi site the increase was less pronounced (from 82.8% in 1990 to 85.9% in 1993), but with also relatively high similarity indexes.

Effects of treatments on species diversity

The effects of different treatments on species diversity are presented in Table 2 and 3. At the Yishi site, surface disturbance and removal of perennials caused an increase in species diversity that was significant for three years after the treatment (Table 2, D-E). Herbicide applications on cleared surfaces caused a decrease in species diversity, proportional to the dose of simazine, that remained significant for two years after the treatment (A, B, C < D, Table 1). In the fourth year, similar diversity values as in

Table 1. Comparison of Sorensen's similarities indexes (%) between pairs of treatments at the Yishi and Matta experimental sites. A: Clearing + simazine treatment before planting and a year after (5 kg/ha). B: Clearing + simazine treatment only before planting (5 kg/ha), C: Clearing + simazine treatment before planting and a year after (2.5 kg/ha), D: Clearing with simazine treatment omitted, E: Control (no clearing nor simazine treatments)

Pair of treatments	Yishi site				Matta site		
	1990	1991	1992	1993	1991	1992	1993
A-B	84.8	77.6	86.5	85.7	71.1	74.9	95.8
A-C	83.3	83.4	86.1	88.5	72.9	75	95.1
A-D	81.6	74.9	84.1	87.5	71.7	77.2	97.2
B-C	83.2	84.1	88.9	85	76.1	72.2	95.8
B-D	81.5	81.6	88.2	86.7	71.1	71.4	98.6
C-D	82.6	82.7	88.6	88.8	75.9	76.3	97.9
D-E	82.4	78.5	83.1	79.4	77.5	74.1	88.5

Table 2. Shannon-Wiener diversity index (H') for different treatment at Yishi site in 1990/93. T-test for H' index, between pair of treatments. A: Clearing + simazine treatment before planting and a year after (5 kg/ha). B: Clearing + simazine treatment only before planting (5 kg/ha), C: Clearing + simazine treatment before planting and a year after (2.5 kg/ha), D: Clearing with simazine treatment omitted, E: Control (no clearing nor simazine treatments). * indicates $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ and NS, not significant

Treatment	1990					1991					1992					1993				
	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
H' index	2.96	2.98	3.29	3.34	3.01	2.48	2.90	2.92	3.22	2.56	3.19	3.29	3.17	3.25	2.77	3.02	3.26	3.14	3.22	2.69
Pair of treatments	T		Significance		T		Significance		T		Significance		T		Significance					
A-B	0.129		NS		3.530		**		0.859		NS		0.243		NS					
A-C	2.173		*		3.441		**		0.222		NS		0.556		NS					
A-D	2.649		*		7.602		***		0.560		NS		0.606		NS					
B-C	2.268		*		0.166		NS		1.060		NS		0.280		NS					
B-D	2.825		*		3.714		**		0.384		NS		0.342		NS					
C-D	0.407		NS		3.076		*		0.791		NS		0.076		NS					
D-E	3.715		**		7.392		***		5.047		***		1.662		NS					

Table 3. Shannon-Wiener diversity index (H') for different treatment at Matta site in 1991/93. T-test for H' index, between pair of treatments. Key legends as in Table 2.

Treatment	1991					1992					1993									
	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E					
H' index	2.14	2.21	2.51	2.80	2.10	2.01	1.88	2.18	2.52	2.11	2.74	2.80	2.85	2.87	2.18					
Pair of treatments	T					Significance					T					Significance				
A-B	0.301					NS					0.622					NS				
A-C	1.706					NS					1.151					NS				
A-D	2.828					*					2.581					*				
B-C	1.284					NS					1.276					NS				
B-D	2.368					*					2.379					*				
C-D	1.267					NS					1.472					NS				
D-E	3.757					**					2.001					NS				

the third year were recorded, but the difference between the cleared and uncleared controls was no longer significant.

At the Matta site, a similar pattern for species diversity was observed (Table 3). Species diversity was increased by the clearing and reduced by the herbicide treatments operations during the first two years. Significant species diversity differences were observed during the first season between treatments that received high doses of herbicide and the no-simazine control treatment (A-D and B-D), as well as between the cleared and uncleared treatments (D-E). During the second year a general decrease of species diversity was observed. Significant diversity differences were found between high-simazine and no-simazine plots. In the third year higher diversity values were noted among all treatments, but significant differences in diversity was found only between the clearing treatment (D) and the uncleared control (E), not between simazine treatments.

Plant cover

At the Yishi site, in the first year, removal of perennial vegetation and associated surface disturbance caused a significant increase in total plant cover (including herbaceous plants), compared with the uncleared control (D-E, Fig. 2a). Simazine applications at any dose on disturbed areas, significantly reduced plant cover (A, B, C), back to levels similar to those found in undisturbed control (E).

In the second year after the treatment, total plant cover was similar in the uncleared control and in cleared sites with moderate or no simazine applications doses, but was significantly lower in sites which had received a high simazine dose in both years (A). In the third and fourth year after the dis-

turbance operations, plant cover was similar in all treatments and no significant differences were noted.

At the Matta site, the clearing operations significantly reduced plant cover compared to the uncleared control in the first year. Simazine applications in the cleared sites, further significantly reduced plant cover (Fig. 2b). These differences

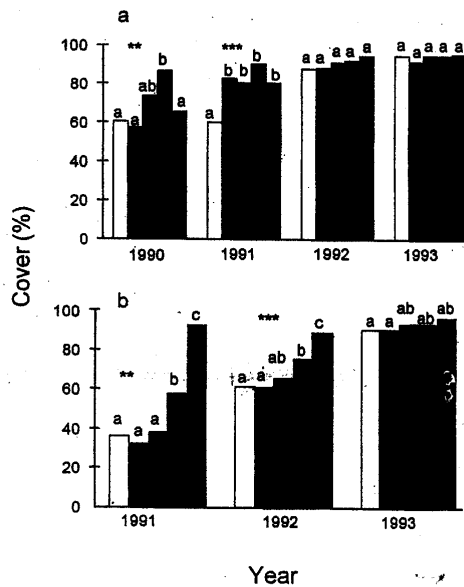


Fig. 2. The effects clearing and simazine treatments on plant cover at (a) Yishi site and (b) Matta site. Treatments: A (□), B (■), C (■), D (■) and E (■). Key to clearing and simazine treatments as in Fig. 1.

remained significant during the second year. In the third year, no significant differences in plant cover among treatments were found.

Life forms

At the Yishi site, clearing drastically decreased the relative cover of chamaephytes in the first year. Most of the space released was taken up by a significant increase in therophytes (Fig. 3a). With one exception, the difference in therophyte relative cover between cleared and uncleared treatments remained significant until the fourth year. Significant reductions in therophytes relative cover due to the second simazine application were observed in the second year, but disappeared in the subsequent years. Chamaephyte relative cover was not affected by simazine.

Clearing treatments enhanced geophyte presence during the first seasons, showing significant differences between the disturbed and the control areas

(1991: $F_{4,40} = 3.94, p > 0.01$, 1992: $F_{4,40} = 2.85, p > 0.05$). During the first three seasons significantly higher geophytes values were obtained in the herbicide treatments (13% relative cover in treatment A compared to 7% in D). In the last season this effect was still apparent but no longer significant.

Hemicryptophytes and phanerophytes (minor elements in these communities) showed no significant differences between treatments in all survey seasons.

At the Matta site, significant differences between treatments in the relative cover of life forms were seen only during the first year. Chamaephytes cover decreased, while therophytes cover significantly increased in cleared areas with no herbicide application (D). Hemicryptophytes cover significantly increased ($F_{4,40} = 5.33, p > 0.01$) in the first year in cleared sites compared to controls (A, B, C, D > E). Geophytes significantly increased in the first year ($F_{4,40} = 4.95, p > 0.01$) in sites where high simazine doses were sprayed, compared to areas where herbicide was not applied (A, B > D, E).

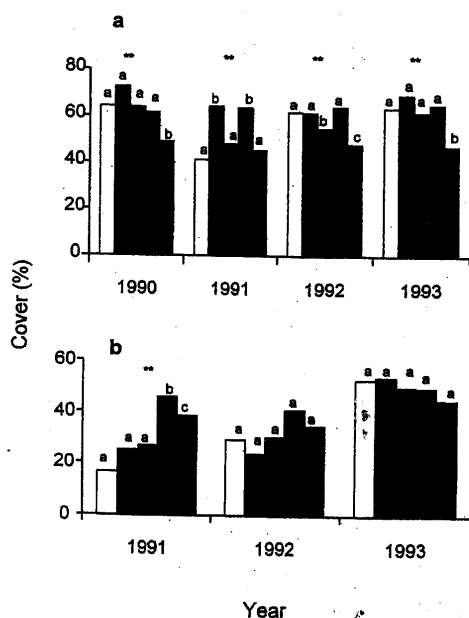


Fig. 3. The effects clearing and simazine treatments on cover of therophytes at Yishi and Matta sites (a and b, respectively). Treatments: A (□), B (■), C (▒), D (▓) and E (■). Key to clearing and simazine treatments as in Fig. 1.

Responses of individual species

The cover of many individual species showed significant responses to the clearing and/or simazine treatments. A cross-classification of species into herbicide and clearing response groups, based on the results of 1990, 1991, 1992 and 1993 for the Yishi and Matta site is shown in Table 4.

At Yishi, many species of therophytes, geophytes and hemicryptophytes showed positive responses to clearing, while some chamaephytes showed the expected negative response. A large group of species showed a negative response to simazine with a positive or no consistent response to clearing. The simazine sensitive species were mainly annuals of the Papilionaceae, Gramineae and Asteraceae families, but also some hemicryptophytes. There was a small but substantial group of species that increased in response to simazine, mostly therophytes and geophytes.

At Matta, fewer species showed consistently significant responses to either clearing or simazine treatments.

The comparison between the herbicide increased (H+) and reduced (H-) groups showed a higher number of species that were negatively affected (H-) by simazine applications. No significant association was found between life forms and herbicide response groups ($\chi^2: 4.158; df: 3; p >$

0.235). The chi-square test analysis between the clearing increased (C+) and reduced (C-) groups, showed significant life forms differences (χ^2 : 21.55; df : 3; $p > 0.001$). A higher number of therophytes, hemicryptophytes and geophytes were enhanced by the removal of aboveground structures of perennial vegetation, while chamaephytes tended to be negatively affected by clearing.

Three dominant plant species, with different responses to the treatments, were selected from the individual response analysis in order to characterize the general vegetation dynamics.

The annual *Ainsworthia trachycarpa* Boiss. (Umbelliferae) is a simazine-enhanced species, which showed a clear correlation between the intensity and type of disturbance and its relative cover (Fig. 4a). During 1990 and 1991 an increase in *A. trachycarpa* cover was observed, particularly in the herbicide treatments. At the same time, an opposing response process was noted in *A. sterilis*, a simazine

sensitive annual grass, which however did increase in the clearing treatment D (Fig. 4b). During the last two seasons the process at the herbicide sites reversed; *A. trachycarpa* cover decreased, and that of *A. sterilis* increased. By 1993, the relative cover of *A. trachycarpa* and *A. sterilis* in simazine sites had returned close to, but not quite reached the values in control sites. *S. spinosum*, the dominant dwarf shrub species of these communities, was negatively affected by the clearing operations (Fig. 4c). Recovery was somewhat faster in the sites where simazine has been applied, but was far from complete in any of the treatments in the fourth year.

Discussion

The clearing and herbicide applications had a major impact on the dynamics of early successional communities in newly planted forests. The clearing and simazine applications opened new sites, released competition from dominant species and increased spatial heterogeneity. This permitted the colonization and establishment of species that were favoured by the disturbance operations (Denslow 1985; Pickett & White 1985; Halpern 1988). The significant increase in species richness and diversity observed in the cleared treatment (D), during the first years at both experimental sites, was probably related to the increase in resources availability (i.e., light and water) as perennial dominants were removed (Armesto & Pickett, 1985). Annuals and geophytes, competitively suppressed by perennials, could establish themselves, thus increasing the number of species at these sites. During the fourth season at the Yishi site, spatial heterogeneity was reduced as general cover of the dominant species increased. Consequently, significant differences in species diversity between the cleared and uncleared control (D-E) were no longer evident.

In the sites where simazine was applied species richness and diversity was significantly reduced during the first two years (Tomkins & Grant, 1977). The herbicide treatment initially suppressed many simazine-sensitive species (mainly annuals of the Papilionaceae, Gramineae and Asteraceae families, but also some hemicryptophytes). The increase in species richness and diversity and the disappearance of significant differences among treatments during the third and fourth years, was an indication of the resilience capability of these communities after disturbance (Noy-Meir & Walker, 1986).

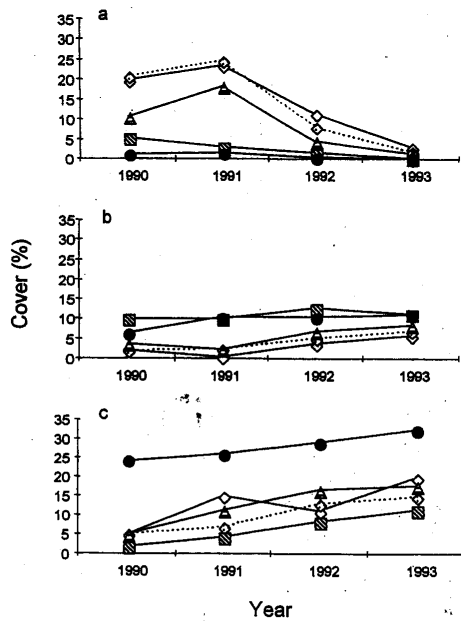


Fig. 4. Changes in cover of *Ainsworthia trachycarpa* (a), *Avena sterilis* (b) and *Sarcopoterium spinosum* (c), at Yishi site. Treatments: A (◇), B (◊), C (▲), D (■) and E (●). Key to clearing and simazine treatments as in Fig. 1.

Following clearing, tall annual species, such as *A. sterilis* were probably recruited from the seed bank and gained dominance due to reduced competition with perennial vegetation (mainly dwarf shrub species). In sites where simazine was applied (A, B, C) herbicide-enhanced species such as *A. trachycarpa* gained dominance. Recruitment from seed bank, and reduced competition from herbicide-sensitive species (e.g. *A. sterilis*), in the absence of perennial and other annual plants, were likely to be responsible for this phenomenon. However, these changes in plant composition were mostly transient. As the influence of clearing and of the herbicide decreased, species dominants previous to the disturbance were restored to their previous dominant position. *S. spinosum*, the main dwarf shrub species of these communities, regenerated vegetatively and became dominant once again. Grasses were recruited by seed rain from the adjacent non-herbicide quadrats, while legumes were restored from persistent seed banks. The high floristic similarity indexes between treatments found at both sites, also indicated that the disturbance operations did not change the qualitative characteristics of the community. However, important temporal changes in the quantitative proportions of the species present at the sites were noted.

The tree saplings, three and four years after being planted, have on average a height of half a meter (Sternberg, 1994). Their presence at the time this study ended had no important influence on the natural vegetation. Full details on the effects of clearing and herbicide treatment on coniferous seedling establishment and growth will be presented elsewhere, but we can briefly mention that seedling mortality significantly increased with decreasing intensities and frequencies of simazine applications. In plots where treatment A was applied (standard management practices), seedling survival rates were on average around 65%, compared to 20% survival in sites where the herbicide was not applied (treatment D).

The characteristic of resilience in the disturbed sites was determined by the life history attributes of the dominant species (Noble & Slatyer, 1980; Armesto & Pickett, 1985). Plant morphology traits such as bud position allowed plant species to overcome the disturbances. For example, chamaephytes (the main life form at these communities) have their perennating buds close to the soil surface. Thus, they are able to resprout after the

removal of aboveground structures. The storage of resources into roots and remaining stems allowed high re-growth rates and a rapid reoccupation of the area. *S. spinosum* recovery was an example of this process. Geophytes and hemicryptophytes also overcame disturbance as their buds were located underground or close to the soil surface. The herbicide-sensitive species (H-, Table 4) were able to recolonize sites where simazine was applied three and four years after its application, overtaking other species that were originally enhanced by the herbicide, and to re-establish their dominance. The main mechanisms involved in this phenomenon included seed rain of herbicide-sensitive species from adjacent non-herbicide plots (treatment D and E), germination from persistent seed banks (mostly legumes) (Russi *et al.*, 1992) and the gradual decomposition and disappearance of the herbicide from the soil (Koehler, 1983). Annual grasses (also herbicide-sensitive) characterized by high growth rates and high reproductive resource allocations were able to outcompete and displace the simazine favoured species.

The results for both experimental sites showed a general trend toward successional convergence among treatments, as community properties become more similar with time (Glenn-Lewin & van der Maarel, 1992). The life history attributes enabling the dominants to survive in the seed bank or reproduce vegetatively after disturbance were relevant in determining the successional convergence observed in the experimental sites. These traits are considered common in plants of the Mediterranean region, with a long history of exposure to disturbance (Naveh, 1975, 1990).

The present study provides meaningful insights into the early stages of the dynamics of the natural vegetation in newly planted Mediterranean forests after disturbance by clearing and simazine applications. The current pre-forestation management of these areas appeared to have drastic effects on community composition in the first two years, but the resilient characteristics of the natural vegetation allowed a substantial recovery, in the following two years. The transitory disturbance of the native plant communities may be justified by the need to ensure a high establishment rate of planted trees (Sternberg, 1994). These predictions on community dynamics are relevant only until the interference between the planted trees and the natural vegetation becomes an important factor.

Table 4. Classification of species by significant responses ($p < 0.01$) to herbicide/clearing disturbance at Yishi and Matta site. H-, C-: Abundance usually reduced by herbicide effects and clearing respectively. H+, C+: Abundance usually increased by herbicide effects and clearing respectively. Ho/Hx, Co/Cx: response to herbicide/clearing not detected or not consistent between treatments and years. # Significant all years.

Yishi site			
	H+	Ho/Hx	H-
C+	<i>Ainsworthia trachycarpa</i> # <i>Erodium cicutarium</i> <i>Erodium malacoides</i> <i>Geranium robertianum</i> <i>Mercurialis annua</i> <i>Ononis pubescens</i>	<i>Andrachne telephioides</i> <i>Carthamus tenuis</i> <i>Daucus carota</i> # <i>Dianthus strictus</i> <i>Hordeum spontaneum</i> <i>Linum pubescens</i> <i>Notobasis syriaca</i> <i>Ranunculus asiaticus</i> # <i>Sinapis alba</i> <i>Vicia palaestina</i>	<i>Alopecurus utriculatus</i> <i>Anagallis arvensis</i> <i>Biscutella didyma</i> # <i>Hordeum bulbosum</i> <i>Nigella arvensis</i> <i>Pimpinella cretica</i> <i>Silybum marianum</i> <i>Thrinicia tuberosa</i>
C0/ Cx	<i>Anchusa strigosa</i> <i>Conyza canadiensis</i> <i>Colchicum stevenii</i> <i>Nigella arvensis</i> <i>Ononis reclinata</i> <i>Plantago afra</i> <i>Scilla autumnalis</i> <i>Theligonum cynocrambe</i> <i>Torilis tenella</i> #	<i>Alcea acaulis</i> <i>Hirschfeldia incana</i>	<i>Alopecurus arundinacea</i> <i>Anthemis hebronica</i> <i>Anthemis pseudocotula</i> <i>Asteriscus spinosa</i> <i>Avena sterilis</i> # <i>Bromus fasciculatus</i> <i>Centaurea crocodylium</i> <i>Crepis sancta</i> <i>Crupina crupinastrum</i> <i>Heptasteru crenata</i> <i>Helichrysum sanguineum</i> <i>Lotus peregrinus</i> <i>Phagnalon rupestre</i> # <i>Pisum sativum</i> <i>Poa bulbosa</i> <i>Trifolium campestre</i> <i>Trifolium constantinopolitan.</i> <i>Trifolium lappaceum</i> <i>Trifolium purpureum</i> <i>Vicia ciliata</i> <i>Vulpia myuros</i>
C-		<i>Chilidenus iphionoides</i> <i>Majorana syriaca</i> <i>Micromeria nervosa</i> <i>Sarcopoterium spinosum</i> #	
Matta site			
	H+	Ho/Hx	H-
C+	<i>Ainsworthia trachycarpa</i> <i>Medicago orbicularis</i>	<i>Carlina curetum</i>	<i>Anagallis arvensis</i> <i>Arrhenatherum palaestinum</i> <i>Mercurialis annua</i> <i>Piptatherum holciforme</i> #
C0Cx		<i>Poa bulbosa</i>	<i>Avena sterilis</i> # <i>Bromus fasciculatus</i> <i>Helianthemum salicifolium</i> <i>Lagoecia cuminoides</i> <i>Phagnalon rupestre</i> <i>Pisum fulvum</i>
C-		<i>Aegilops peregrina</i> <i>Daucus carota</i> <i>Sarcopoterium spinosum</i> #	

The results also showed the importance of adjacent non-herbicide plots in the relative fast recovery of both experimental sites, since they provided seed rain sources of herbicide-sensitive species. Although not particularly covered in this study, we believe that on a larger scale, the inclusion of non-herbicide strips within large afforested areas, or the local application of herbicide only around planted trees, could increase edge effects and provide further sources for seed rain, enabling a faster restoration of the areas. Further studies including larger areas than covered by the present study and potential of herbicide secondary effects such as the contamination of underground water levels (Glenn & Angle, 1987; Stearman & Wells, 1997) or changes in the invertebrate community (soil macro and microfauna) (Prasse, 1985), may provide a wider view of the effects of herbicide applications on ecosystem functioning in afforested areas of the Mediterranean region.

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