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Variation in leaf phenology and habit in *Quercus ithaburensis*, a Mediterranean deciduous tree

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Summary

1 The phenology of leaf abscission and leaf flushing were studied in four populations of *Quercus ithaburensis* Decne., a deciduous oak tree, during four seasons in Israel.

2 Phenological variation among the individual trees was very high in all populations. Some trees were clearly deciduous, while others had only a short duration of leaflessness. In some trees the end of leaf abscission took place after leaf emergence; such individuals could be considered as evergreen.

3 The populations differed in their phenological behaviour among sites and seasons, and there were interactions between these factors.

4 The differences in the phenological variables of each population among the four seasons and the correlation between them and the correspondent climatological data from nearby stations indicated that climate-cued phenotypic plasticity was one of the causes of the observed variation in the phenology of the populations.

5 A high and significant correlation was found between the phenological variables of each individual tree among the four seasons. This means that each individual tree kept a similar phenological pattern in spite of the phenological differences among the populations and the seasons. This indicates that genotypic variation might be a cause of the observed variation in the phenology of individual trees.

6 A hypothesis that this species may be in an evolutionary transition from deciduous toward evergreen leaf habit is proposed. This might provide an alternative explanation for the origin of some evergreen Mediterranean trees.

Keywords: deciduous, evergreen, leaf habit, leaf longevity, Israel, Mediterranean, phenology, *Quercus ithaburensis*

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Introduction

Deciduous forests are the typical vegetation of the temperate regions of the world and of the middle belt of high mountain forests. The deciduous leaf habit probably evolved as a drought avoidance mechanism (Axelrod 1966; Kozlowski 1976). Moore (1980), Chabot & Hicks (1982) and Kikuzawa (1989), compared the advantages of the evergreen and deciduous habits and how those adaptive differences can be related to distributional patterns and climatic gradients. Mediterranean type forests in different parts of the world are dominated by evergreen sclerophyllous trees and shrubs (Naveh 1967; Mooney & Dunn 1970a; Raven 1971; Aschman 1973; Cody & Mooney 1978; Orshan 1986, 1989), with long leaf lifetime (Moore 1980; Field & Mooney 1983).

In most plant species leaves are shed when low temperatures and short day length prevent net photosynthesis (Larcher & Bauer 1981). However, winter

in Mediterranean climates is mild and wet (Mooney *et al.* 1974; Quezel 1985), and under these conditions net photosynthesis is also possible in winter. Mooney & Dunn (1970a,b) found positive carbon budgets all year round in evergreen Californian chaparral species. In the Mediterranean species, *Quercus ilex*, *Q. pubescens* and *Olea europea* (Larcher & Bauer 1981) and *Arbutus unedo* (Beyschlag *et al.* 1990) the photosynthetic rate in the winter is only a little lower than in summer, and in *Cistus salvifolius* it is higher in winter (Harley *et al.* 1987). The cambial activity of adapted Mediterranean evergreens commences in the autumn when temperatures drop and the rainy season starts, lasting until the early summer when drought stress and high temperatures prevail (Lipshitz & Lev-Yadun 1986). At lower altitudes in Israel, the winter is an intensive growing season and the flowering time for many annuals, whereas deciduous trees are dormant. Thus Mediterranean evergreen trees may have an adaptive advantage over deciduous ones

growing in the same habitat. It is therefore expected that elongation of the leaf life span into the favourable winter season will be of positive adaptive value for a deciduous Mediterranean tree.

Evergreen trees have a relative advantage over deciduous trees in nutrient deficient soils (Goldberg 1982; Jonasson 1989), and in environments where low nutrient levels limit leaf growth (Chabot & Hicks 1982). Mediterranean soils are known to be nutrient poor and evergreen habit should be preferred (Shaver 1981). Kikuzawa (1989) found that evergreen trees are indeed more common in high stress sites, while deciduous trees grow in the favourable ones. However, about 45% of the tree species in the Mediterranean forest of Israel are deciduous (Shmida 1983). This can be explained by migration from adjacent phytogeographical regions (Danin & Plitman 1989), or as the result of glacial periods (Shmida 1978; Zohary 1973; Pons & Quezel 1985).

The evergreen leaf habit and sclerophyllous leaf type were found to covary with several other plant characters across genera in the woody flora of southwestern Spain. These genera were found to originate in the early Pliocene, which was characterized by a tropical climate (Herrera 1992). The ancient origin of evergreen habit does not, however, exclude its relative adaptive advantage over deciduousness.

Q. ithaburensis is a deciduous tree, although from the previous discussion it would appear that in its natural habitat, evergreenness should be advantageous over deciduousness. The aim of this work was to study leaf phenology of in *Q. ithaburensis* and to develop the hypothesis that this species may be in an evolutionary transition from a deciduous to an evergreen leaf habit, thus providing an alternative explanation for the origin of some of the Mediterranean evergreen trees.

Methods

THE PLANT

Quercus ithaburensis Decne. is an eastern Mediterranean species belonging to the circum-Mediterranean group of *Q. aegilops* oaks (Zohary 1973). Zohary (1972) identified five varieties in the species. All the studied populations belong to var. *ithaburensis*. *Q. ithaburensis* grows in the southern part of Turkey, in a few localities in the Levant and the southern border of its distribution is in Israel (Fig. 1). It is a thermophilous tree growing at altitudes of 0–500 m a.s.l. (Zohary 1973), or rarely up to 1000 m (Kaplan 1984). *Q. ithaburensis* grows on a variety of soils and is associated with the hot and dry southern aspects of hills in lower-Galilee, while the evergreen *Q. calliprinos* grows on the more favourable northern slopes (Aloni & Orshan 1972). High values of transpiration were measured in *Q. ithaburensis* during the summer months (Openheimer 1947), indicating that

its roots go deep and reach wet soil even in the dry summer.

Of the dominant trees in several plant communities that cover large areas of the Mediterranean part of Israel, only *Q. ithaburensis* is deciduous (Zohary 1973). It was an important component of large areas of open forests which were cut down at the beginning of the century (Eig 1933; Zohary 1973).

Several authors (Zohary 1973; Kaplan 1984), noted the wide morphological and phenological variability as well as the irregular leaf habit in *Q. ithaburensis*. Zohary (1973) even wrote 'It may fail to shed its leaves in years of mild winters'.

STUDY AREAS

Four uniform plots with minimum habitat variation, each with about 60 oak trees were randomly chosen. Each one of the plots Hadera, Alonim, Beit-Rimon, and Yehudia represents a different *Q. ithaburensis* population within the northern part of Israel (Fig. 1), on a West to East gradient with increasing distance from the Mediterranean sea, and increasing elevation (see Table 1 for details and climatic data. Additional trees growing in lower Galilee were selected because of their relatively high cover of leaves during winter 1987/88, to give a group called 'evergreens'.

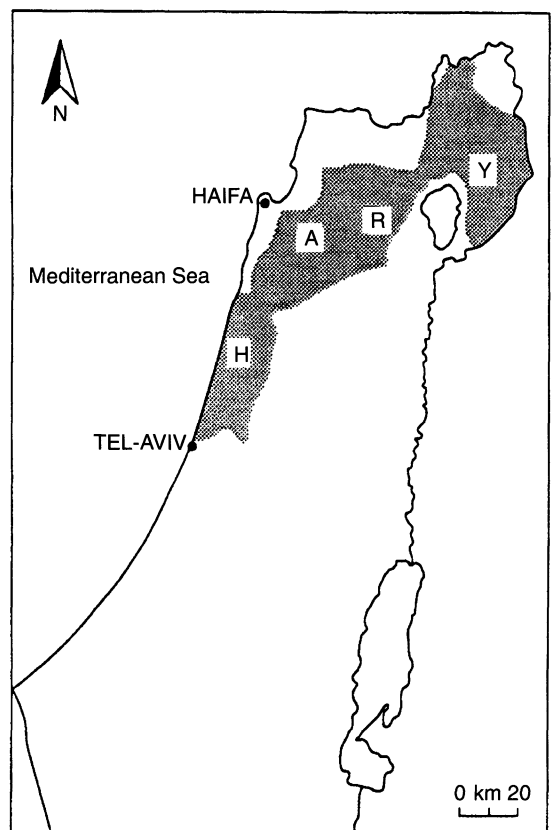


Fig. 1 Distribution map of *Q. ithaburensis* in Israel. The letters indicate the locations of the populations: H = Hadera; A = Alonim; R = Beit-Rimon; Y = Yahudia.

Table 1 Location and environmental conditions of the *Q. ithaburensis* populations under surveillance

Plot	Location	Soil type	Distance from sea (km)	Altitude (m a.s.l.)	Precipitation (mm)	Average daily temperature (°C)	
						January	August
Hadera	Coast plain	sand	10	50	556	12.8	25.9
Alonim	Lower Galilee	alluvium	35	100	578	12.1	26.9
Beit-Rimon	Lower Galilee	alluvium	50	100	521	11.4	26.6
Yahudia	Golan heights	gromosol	90	550	550	8.6	24.5

OBSERVATIONS

All the trees were numbered and then observed every 2–4 weeks during the autumn, winter and spring of 1988/89, 1989/90, 1990/91 and 1991/92, except for Hadera plot which was monitored only through the first two seasons. On each visit the percentage of old or new leaf cover on each tree was estimated visually. Old leaves were those which had emerged during the previous spring or summer, new leaves were those emerging in the current season. In order to compare the different phenological stages in different years, the date was always measured in weeks from the first week of October and the durations of each phenological stage was measured in weeks.

Start of leaf abscission was defined as the first week in which leaf abscission occurred, duration of leaf abscission as the number of weeks between the beginning of leaf abscission and the end of leaf abscission when only a few old leaves were still found on the tree. The duration of leaflessness (the period with no leaves), from the end of leaf abscission until bud bursting and the beginning of leaf flushing, the date of start of leaf flushing, the duration of leaf flushing and the date of the end of leaf flushing were also determined.

DATA ANALYSIS

The value of each phenological variable was determined for each tree. When the date of observation preceded or exceeded the date of a certain variable, the date was estimated by extrapolation. Two-way ANOVA was used to analyse both the effect of the population and the year on the different phenological variables and in particular on duration of leaflessness. When significant interaction occurs between the two factors in the analysis it is misleading to average the effects of one factor over all the levels of the second one (Underwood 1981). Therefore the results of one-way ANOVA followed by an posteriori comparison for each factor is not presented.

The values of all the phenological variables were found to be significantly intercorrelated. Therefore not all variables are presented in each figure and table. Stepwise multivariate regression analysis was performed in order to find out which variables were most important in their influence on the duration of leaflessness.

The correlation between the value of each phenological variable of each individual tree in the different years was tested by calculation of the Pearson correlation coefficient.

Correlations were calculated between the phenological variables and corresponding meteorological data, in order to find possible connections. Meteorological data from stations located nearby the plots were received from The Meteorological Service of the State of Israel.

All analyses were performed using GLM, CORR, and REG procedures provided by SAS (SAS Institute 1988).

Results

LEAF PHENOLOGY OF INDIVIDUAL TREES

The individual trees had very different phenologies. The earliest start of leaf abscission was observed in the first week of October, while the latest was at the beginning of March. In order to demonstrate the large differences among individuals, Fig. 2 presents the patterns for two extreme trees. In the first tree (Yehudia 108 observed in 1991/1992) leaf abscission ended 14 weeks before the start of leaf flushing, thus duration of leaflessness was 14 weeks and the corresponding graph is U-shaped. In the second tree (Hadera 515) the end of leaf abscission was 11 weeks later than the start of leaf emergence and the corresponding graph is X-shaped, illustrating that leaf cover was never less than about 10% and that this tree was, at least in 1989/1990, evergreen. 'Evergreen' trees in which the start of leaf flushing preceded end of leaf abscission

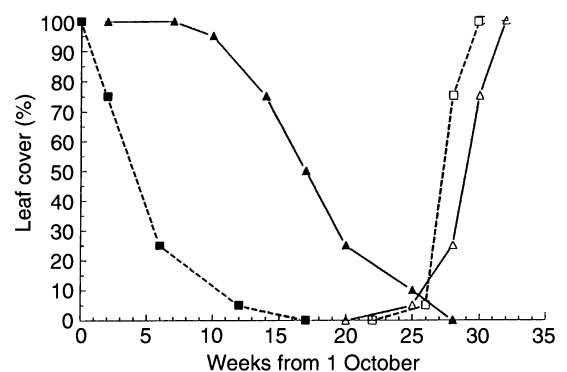


Fig. 2 Leaf phenology of two extreme trees. 'Yahudia 460' in 1991/92 (■, old leaves; □, new leaves) and 'Hadera 515' in 1989/90 (▲, old leaves; △, new leaves).

Table 2 Pearson correlation coefficients (r) for the correlations of each of the phenological variables: start of leaf abscission (SA), duration of leaf abscission (DA), end of leaf abscission (EA), duration of leaflessness (DLL), start of leaf flushing (SFL), duration of leaf flushing (DFL), and end of leaf flushing (EFL) of individual trees among the years 89 ($n = 248$), 90 ($n = 248$), 91 ($n = 190$), and 92 ($n = 188$)

var.	SA89	SA90	SA91	var.	DA89	DA90	DA91
SA90	0.74***			DA90	0.48***		
SA91	0.57***	0.62***		DA91	0.24**	0.34**	
SA92	0.59***	0.60***	0.78***	DA92	0.12ns	0.24*	0.34***
var.	EA89	EA90	EA91	var.	DLL89	DLL90	DLL91
EA90	0.43***			DLL90	0.64***		
EA91	0.34***	0.34***		DLL91	0.22**	0.26**	
EA92	0.35***	0.38***	0.51***	DLL92	0.36***	0.42***	0.55***
var.	SFL89	SFL90	SFL91	var.	DFL89	DFL90	DFL91
SFL90	0.47***			DFL90	0.28***		
SFL91	0.64***	0.74***		DFL91	-0.09	-0.11	
SFL92	0.22**	0.38***	0.41***	DFL92	0.20**	0.31***	0.11
var.	EFL89	EFL90	EFL91				
EFL90	0.525***						
EFL91	0.63***	0.63***					
EFL92	0.40***	0.48***	0.72***				

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

were found in all plots. These trees represented 1.7%, 14.6%, 14.7%, and 41% of the populations in Beit-Rimon, Yehudia, Alonim and Hadera respectively and this proportion was negatively correlated with the duration of leaflessness.

The correlation analysis between the values of each phenological variable in all pairs of seasons (Table 2), showed that 39 out of 42 such pairs were significantly correlated. The duration of leaflessness (DLL), the most important variable, showed a high and significant correlation.

LEAF PHENOLOGY AT THE POPULATION LEVEL

The pattern of leaf phenology at the population level (Fig. 3), resembled the pattern of the individual trees (Fig. 2). In 1991/92 the Beit-Rimon population had a deciduous leaf fall pattern in which leaf emergence began well after leaf abscission had been completed and there were no longer old leaves on the trees, giving a U-shaped graph (Fig. 3). In the Hadera population in 1988/89 leaf emergence began before leaf abscission ended, so that at least some leaves could be found on some of the trees throughout the winter, giving an X-shaped graph. The patterns in the Alonim and Yahudia populations were intermediate.

Significant differences were found in all phenological parameters when comparing different populations and seasons (Fig. 4, Table 3). It was not possible to separate the effect of the two factors since their interaction was significant for all variables (Table 3). The Beit-Rimon population was the last to

start leaf abscission but since the duration of leaf abscission was relatively short, the result was a long duration of leaflessness. Differences in leaf flushing parameters were smaller than those for abscission and fall (Fig. 4). The coefficient of variation ($CV = SD/mean$) was lower for the duration of leaflessness in Beit-Rimon (37.8%) than in any other population (74.1–207.3%). The coefficient of variation of the grand mean, over all populations and over all seasons, was also smaller for start and end of leaf flushing (13.2% and 6.7%, respectively), than for start and end of leaf abscission (50.8% and 16.8%, respectively). The Hadera population had the shortest duration of leaflessness.

Correlation analysis among all the phenological variables of each tree over all populations and all sea-

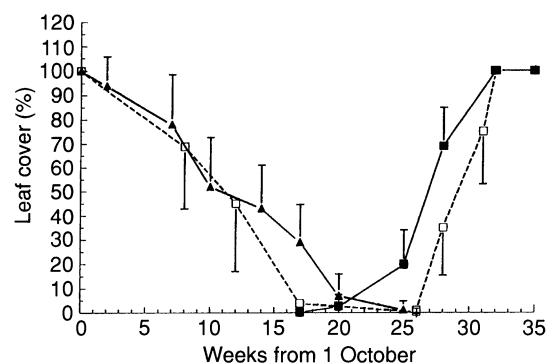


Fig. 3 Leaf phenology of two *Q. ithaburensis* populations. 'Beit-Rimon' in 1991/92 (■, old leaves; □, new leaves - - -) and 'Hadera' in 1988/89 (▲, old leaves; △, new leaves —). Error bars represent standard deviation.

Table 3 Two-way ANOVA comparing aspects of leaf phenology (see Table 2 for abbreviations) across the populations (POP) and the different years (YEAR). All terms are significant at $P < 0.01$

Source of variation	Mean squares						
	d.f.	SA	DA	EA	DLL	SFL	DFL
r^2		0.62	0.42	0.50	0.57	0.76	0.66
Model	17	457	283	300	507	365	250
POP	4	1498	662	469	1075	933	355
YEAR	3	414	551	856	1188	245	778
POP X YEAR	10	53	51	65	76	173	49
Error	856	6	8	6	8	2	2

sons ($n = 874$) revealed significant Pearson correlation coefficient for all except the pair end of abscission and end of flushing. Duration of leaflessness was best correlated with the end of abscission and start of flushing (Table 4).

Correlation coefficients between the population means of start of abscission, end of abscission, and duration of leaflessness each year and average daily minimum and maximum temperatures from September till April are presented in Table 5. Duration of leaflessness was significantly and negatively correlated with daily maximal temperatures of December, January and February. The same climatological variables were also correlated with the end of leaf abscission. Start of leaf abscission was significantly correlated with some of minimal and maximal temperatures of autumn months. No other significant correlations were found in the analysis. No correlation was found between any phenological variable and the total precipitation of the previous year.

Discussion

The comparison of the four populations revealed different patterns of leaf phenology among populations and seasons, but the statistical analysis could not separate the relative importance of each factor (Table 2).

The Hadera population which is at the lowest altitude and is the nearest to the sea, has the mildest weather conditions (Table 1). Although wide variation occurred among the individual trees, duration of leaflessness in this population was the shortest, and the proportion of 'evergreen' trees was the highest. Beit-Rimon had the longest duration of leaflessness, was the most homogeneous among all populations and included the lowest proportion of 'evergreen' trees. Alonim and Yahudia populations represent an intermediate situation in most of the phenological variables, although Alonim is similar in location and climate to Beit-Rimon and Yahudia is more extreme particularly in winter temperatures. The extreme pat-

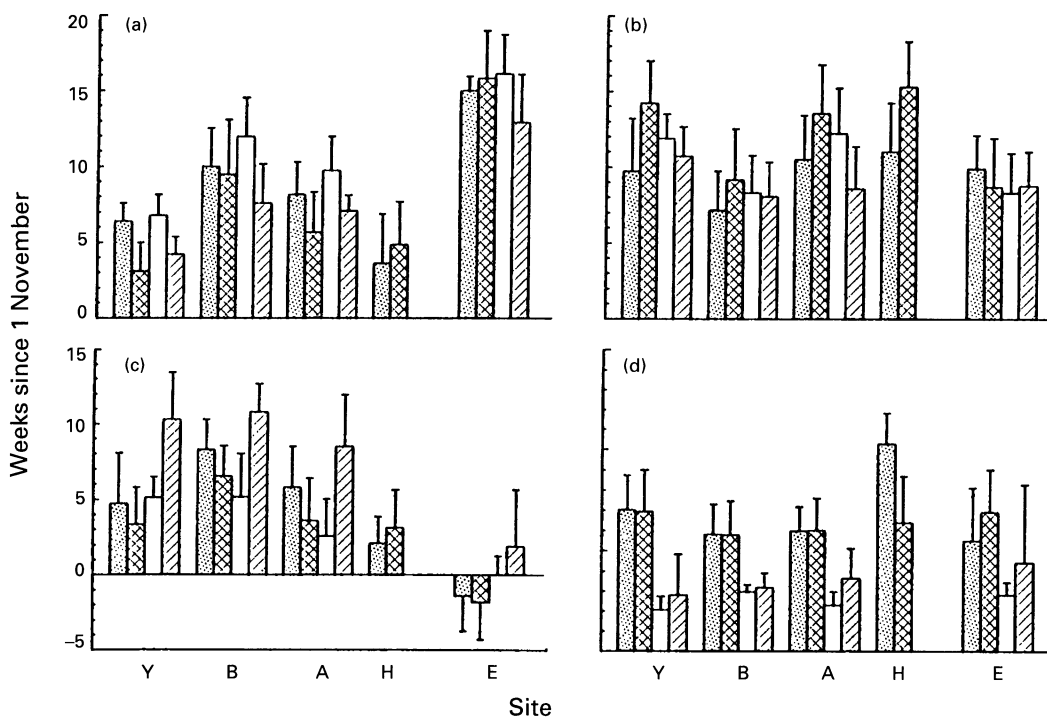


Fig. 4 Comparison of leaf phenology at different sites in different years: (□) 1988/89; (▨) 1989/90; (□) 1990/91; (▩) 1991/92. (a) Start of leaf abscission; (b) duration of leaf abscission; (c) duration of leaflessness; (d) duration of leaf flushing. Error bars represent standard deviation. Y, Yahudia; B, Beit-Rimon; A, Alonim; H, Hadera; E, Evergreens.

Table 4 Pearson correlation coefficients (r) for the correlations among all the phenological variables of individual trees over all populations and all years ($n = 874$). See Table 2 for abbreviations

var.	DA	EA	DLL	SFL	DFL	EFL
SA	-0.58***	0.49***	-0.08*	0.43***	-0.28***	0.28***
DA	1.0***	0.41***	-0.54***	-0.28***	0.16***	-0.243***
EA		1.00***	-0.69***	0.17***	-0.15***	0.06
DLL			1.00***	0.60***	-0.46***	0.32***
SFL				1.00***	-0.80***	0.49***
DFL					1.00***	0.13***

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

tern of Beit-Rimon may have been due to local topography which caused cold air drainage and low winter temperatures, not recorded by nearby meteorological stations (Table 1).

The phenological differences among populations and among individuals may be of genotypic origin, or may reflect phenotypic plasticity (West-Eberhard 1989) caused by climatological and edaphic differences among populations and microhabitat differences among the individuals within each population. West-Eberhard (1989), emphasized the ecological and evolutionary importance of phenotypic plasticity: 'Plasticity itself is a trait subject to natural selection It means that per generation there will be a greater variety of phenotypes available for selection than there are genotypes.' Classification of variation as of genotypic or phenotypic origin can be achieved by experiments in which the same genotype is transplanted into various locations. However this is almost impossible with long lived trees and clues as to the origin of the phenological variation of *Q. ithaburensis* must be found in other ways.

Previous work on other species of oak has shown that genetic variation among individual trees is

Table 5 Pearson correlation coefficients (r) for the correlations between the mean of SA, EA, and DLL of each population each year and average daily minimum and maximum temperatures in September until April. See Table 2 for abbreviations

Variable	SA	EA	DLL
September min.	0.60*	0.32	0.13
September max.	0.16	-0.03	-0.11
October min.	0.59*	0.18	0.32
October max.	0.58*	0.14	0.39
November min.	0.35	0.58	-0.08
November max.	0.57*	0.71**	-0.21
December min.	0.43	0.43	-0.16
December max.	0.55*	0.79***	-0.64*
January min.	0.40	0.74**	-0.54
January max.	0.52	0.76**	-0.53*
February min.	0.55*	0.75**	-0.17
February max.	0.44	0.65*	-0.70**
March min.	0.73**	0.71**	-0.23
March max.	0.38	0.69**	-0.45
April min.	0.82**	0.53*	-0.01
April max.	0.20	0.07	-0.33

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

present in *Q. ilex* in France (Yacine & Lumart 1988), while Crawley & Akhteruzzaman (1988) found phenological constancy in individuals of *Q. robur* for seven years. For the species studied here 'trees may be found at different transition stages, a phenomenon which is one of the expressions of genetic variability in *Q. ithaburensis*' (Kaplan 1984, referring to the Yahudia forest in Israel) and differences in form, size and shape of cupule and gland have been described within var. *ithaburensis*, which makes up all the populations of the present study (Zohary 1972). Such morphological differences may indicate high genotypic variation between populations and individuals.

The populations investigated were homogeneous for altitude, inclination and soil type, minimizing the possible differences in root microhabitat. Genotypic variation can explain the high variability which was observed between individuals within each population. Adjacent oak trees can often be seen in the winter in an alluvial valley, one still with leaves and the second leafless, and this will be repeated every year in the same trees, regardless of the particular temperatures of a certain winter.

Comparison of the phenological behaviour of individual trees among the four years, showed high and significant correlations, in spite of the differences of the population means across the years and among the individuals within each year (Table 2). Individuals with long duration of leaflessness retain this character irrespective of whether the winter is mild or severe. These facts strengthen the possibility that the phenological differences among individual trees within populations are of the genotypic origin.

On the other hand, the variation found among each population mean across the years, seems to be of phenotypic origin. The correlation between the mean duration of leaflessness in the different populations each year and the corresponding autumn and winter temperatures (Table 5) illustrates environment-cued phenotypic plasticity.

Leaf longevity in deciduous trees is less than 12 months (Kikuzawa 1989, 1991); sprouting in winter deciduous species takes place in spring, while leaf shedding occurs in autumn. The timing of leaf emergence and leaf abscission in deciduous trees is environmentally cued, mainly by temperature and photoperiod (Salisbury 1981), but selection may

shorten the dormancy of deciduous trees by causing early leaf emergence or by delaying leaf shed. When new leaves appear on the tree before the old ones are shed and there is an overlap of the new and old leaves, the tree is defined as evergreen. Leaf emergence in *Q. ithaburensis* is an intermediate type, according to the classification of Kikuzawa (1983, 1984), most of the leaves emerging within one month (Kaplan, 1984) between the end of February and the beginning of April. Iwasa & Cohen (1989) predicted that such an early flush of leaf emergence would be optimal for trees at steady state growth in stable environments. Twig elongation with new leaf emergence also occurs in *Q. ithaburensis* in August and September (unpublished observation). This type of growth and leaf emergence is common as a reaction to severe herbivory, for example by *Eriogaster philippii*, or after a forest fire (Kaplan 1984). The last type of leaf emergence fits the Iwasa & Cohen (1989) model for unstable environments. The start, duration and end of leaf flushing in *Q. ithaburensis*, was found to be relatively uniform across populations and seasons; therefore it seems to be a relatively stable trait.

Leaf abscission and duration of leaflessness varied greatly among populations and among individual trees of *Q. ithaburensis*. In contrast to Crawley & Akhteruzzaman's (1988) data for *Q. robur*, no good correlation was found between leaf abscission and emergence, which were independently cued by environmental conditions (Table 5). Leaf abscission was found to be highly correlated with duration of leaflessness. It seems that leaf abscission is the trait most cued by phenotypic plasticity to climatological changes, and in this way is exposed also to natural selection (West-Eberhard 1989). Delay of the end of leaf abscission to a later date than the start of leaf flush may result in overlapping of old and new leaves, leaf longevity of about 12–13 months, and in a change of leaf habit from deciduous to evergreen. If this evolutionary process is completed, at the species level, *Q. ithaburensis* will have changed from a deciduous to an evergreen oak.

Similar leaf longevity of 13–14 months is typical of *Q. calliprinus* (Orshan 1989), *Arbutus andrachne* and *Acer obtusifolium* (syn. *A. syriacum*) (unpublished observation). The genera *Quercus* and *Acer* consist mostly of northern deciduous species with only a few Mediterranean evergreen species. This may be an indication that a transition from deciduous to evergreen leaf habit, under the influence of the Mediterranean climate, has occurred in the past in these and other genera. This may be an alternative explanation for the origin of some of the Mediterranean evergreen trees, which have been assumed to be of palaeotropical origin (Herrera 1992).

Conclusion

The results of the present work are consistent with a hypothesis that *Q. ithaburensis*, in Israel, is in an

evolutionary transition from deciduous toward evergreen leaf habit: This depends on the assumptions that leaf longevity is an adaptive plant character (Kikuzawa 1989, 1991; Chabot & Hicks 1982) and that in Mediterranean climatic conditions and poor soil mineral nutrition, the evergreen leaf habit may have an adaptive advantage over a deciduous one (Mooney & Dunn 1970a; Moore 1980; Goldberg 1982). It also supposes that the individual phenological variation in *Q. ithaburensis* is the result both of genotypic origin and phenotypic plasticity and that phenotypic plasticity as well as genotypic variation are subjected to natural selection and are thus important to initiation, amplification and fixation of changes in plant populations (West-Eberhard 1989).

Only further research on the genetic differences in DNA or proteins, and comparison of growth and reproductive parameters between individual trees with either long or short duration of leaflessness, can fully test the hypothesis.

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