Polymorphisms and environment: the adaptive value of the oil polymorphisms in *Thymus vulgaris* L.

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The present study shows that correlations exist between chemotype polymorphism, sexual polymorphism and the environment. These correlations fall into three categories: 1. a fairly tight correlation exists between soil type and chemotype structure of the thyme populations growing on it; with a soil change, a predictible chemotypic change occurs. 2. There is a clear correlation between a stable environment and low genetic diversity; conversely, in disturbed areas, high genetic diversity exists as indicated by higher outcrossing rates and high levels of chemotype diversity. 3. Thyme uses a strategy of low dispersal which allows, through individual selection, the precise specialisation of each population to its environment.

INTRODUCTION

Thymus vulgaris L. is a perennial labiate which occupies the northern part of the West Mediterranean region. It is a gynodioecious species (Dommée *et al.*, 1978; Assouad *et al.*, 1978) with both hermaphrodite (male fertile) and female (male sterile) individuals occurring in populations.

Reproduction is by seeds (vegetative reproduction never occurs in normal conditions) and a plant can live about 10 to 15 years. Pollination is mainly by bees (Brabant *et al.*, 1980) and the proportion of self-pollination was assumed to vary from 0 to 80 per cent in natural conditions (Valdeyron *et al.*, 1977) and to be dependent on both the genotype and the immediate environment (Dommee, 1981). The migration of pollen (Brabant *et al.*, *loc. cit.*) and seeds (Mazzoni, C. *et al.*, 1985) occurs over short distances and is thus likely to permit genetic differentiation of populations.

Six distinct chemotypes, characterised by differences in the major monoterpenes present, have been recorded for this species. The six monoterpenes were shown to be controlled by a series of loci (Vernet, 1976), with each locus probably having one dominant and one recessive allele. These genes act by favouring different branchings

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in the same biosynthetic chain. Thymol (T) individuals produce nothing but T progeny when selfed, whereas geraniol (G) individuals may produce several chemotypes in the progeny. The greatest genetic diversity for chemotypes is found among progeny from geraniol (G) types, a little less from α-terpineol (A) types, successively less from thuyanol-4 (U), linalol (L) and carvacrol (C) types, and none from thymol (T) (Vernet *et al.*, in press). Granger and Passet (1973) showed that the distribution of the chemotypes does not appear random in their broadscale study of the French mediterranean area; temperature and water were suggested as the active selective factors. The present study demonstrates a correlation between chemotype, sexual polymorphism and environment and an evolutionary interpretation of the oil polymorphisms is presented.
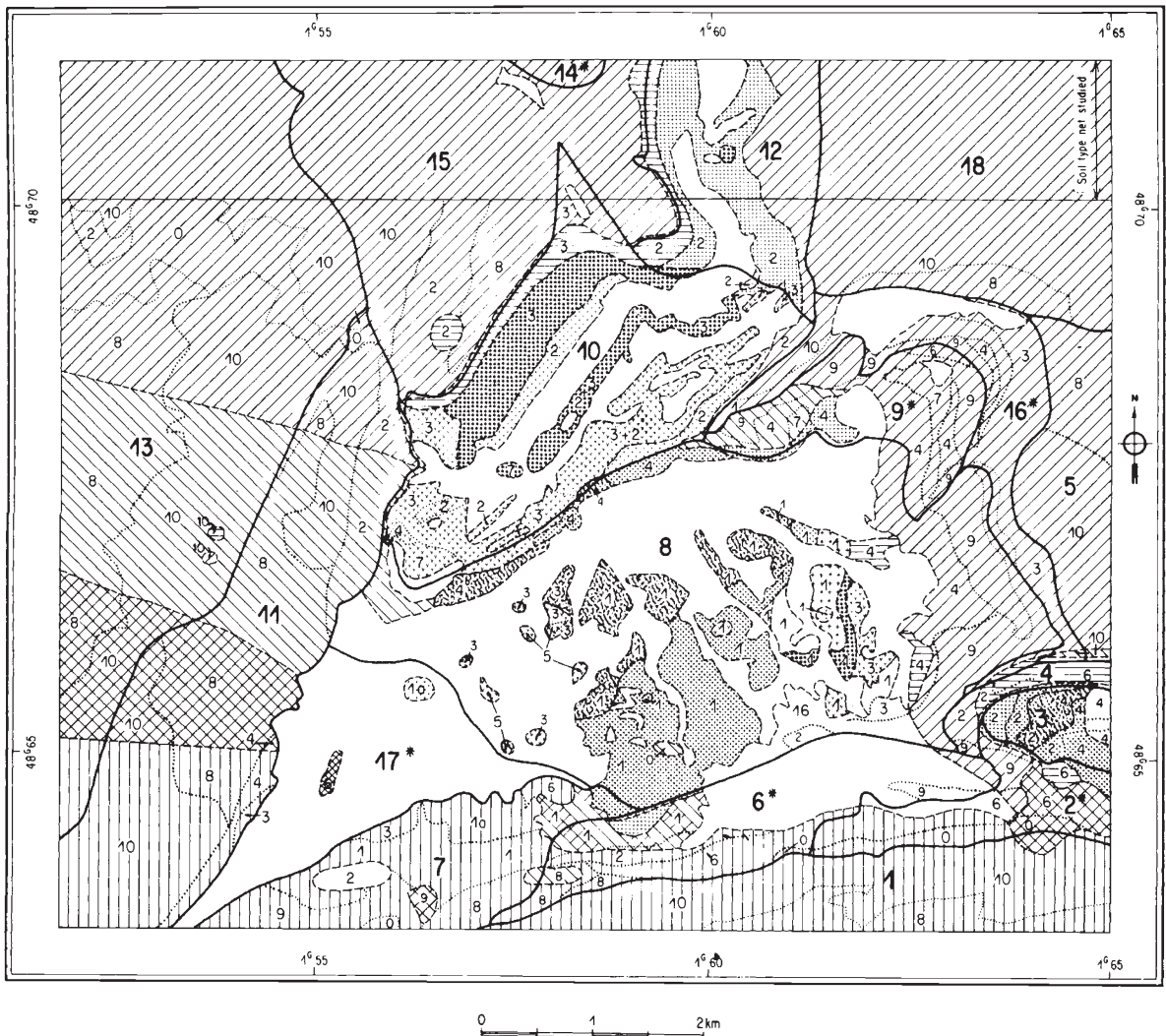
MATERIALS AND METHODS

The distribution of thyme chemotypes was compared with the distribution of, 1. other plant species taken as indicators and, 2. the observed features of the physical environment.

Description of area studied

The area sampled in the present study (fig. 1) is rather restricted (10 × 8 km) and well known to be

Figure 1 Distribution of the chemotypes and of some components of the environment

Numbers 1 to 18 indicate ecological zones (* indicates inadequately sampled zones).

Populations of thyme chemotypes:

CC   LL   UL

TT   CT   LT   AA et AL

TC   CL   LU   GL

TL   LA

The first letter indicates the most abundant chemotype, the second indicates the next most abundant. Two identical letters indicate a pure or almost pure stand. The area left in white contains no thyme population.

Soil types (After the survey and map of the soils of St Martin de Londres by Moinnereau, J. Ecole Nationale Supérieure Agronomique, Montpellier).

0 Rock outcrops on cliffs and steep slopes

1 Regosols and rendziniform calcareous brown soils. Silty clay loams, not stony.
    1(a) calcareous regosols silty sandy loams gravelly and stony.

2 Regosols and redziniform calcareous soils, shallow, clayey silty loams, very stony.

3 Calcareous brown soils, deep, silty clay loams.

4 Calcareous brown soils, shallow, silty sandy loams. Gravelly and very stony; and calcareous regosols and rendzines, shallow, silty clays, stony.

5 Calcareous brown soils and rendzinas, clayey silty loams.

6 Humic rendzinas, silty clay loams, very stony.

7 Calcareous brown soils occasionally darker in pockets, clays; and fersiallitic "sols lessivés", acid, deep, clayey silty loams, very stony.

8 Fersiallitic brown soils, clayey silty loams, very stony; and calcareous fersiallitic soils clayey silty loams, very stony.

9 Fersiallitic calcareous soils, clayey silty loams, stony; and fersiallitic calcareous soils with rock outcrops, silty clay loams, stony.

10 Fersiallitic calcareous soils with rock outcrops, clayey silty loams, few stones.

ecologically diverse, particularly in geomorphology and in soil type. The upland areas of (hard) jurassic and cretaceous limestones divide naturally into three zones separated by other rock types.

The first zone (sectors 1, 2, 6 and 7) constitutes the limestone mountain Pic-Saint-Loup which rises to 658 m, or 450 m above much of the surrounding landscape. The south facing slopes (sector 1) have a very different aspect from those of the north (sector 2). Sector 6 constitutes a very narrow geosyncline at the northern foot of the mountain, geomorphologically quite distinct from sectors 1 and 2. Sector 7 constitutes the northern edge of a plateau of jurassic limestone which extends toward the south.

In the second zone, the western hills were divided into four sectors (11, 13, 14, 15). Sector 11 faces ESE whereas sector 13 faces west and is more exposed to oceanic influences. Sector 14 is exposed to the north and isolated from sectors 11 and 13 by the softer limestone of sector 15.

The third limestone zone (sectors 5 and 18) was divided by shape of the relief and by aspect; sector 18 is a low plateau while sector 5 is slightly inclined toward the north.

Among these three limestone areas are softer secondary and tertiary formations. These are found in three depressions separated by the limestone. The marly bottom (sector 4) of the combe do Fambetou was distinguished from the south-facing northern border (sector 3) and from the north-facing southern border which merges with the Pic-Saint-Loup.

The "furrow" of Notre-Dame-de-Londres (sectors 10 and 12), with its alternating bands of marls and marly limestones running parallel to the valley axis, was divided into sector 12 running N–S, and sector 10 running NE–SW.

The basin of Saint-Martin-de-Londres in the middle of the map is composed of lacustrine limestones and marls in the west (sector 17) and continental deposits of marls and angular conglomerates (sector 8). A band of Lutecian limestone surrounds the basin, separating it from the other depressions and merging with the cretaceous and jurassic limestones of the higher areas around.

At the time of the study, sectors 2, 6, 14 and 16 were not adequately sampled. Thyme was only rarely found growing in sector 9 because of the silicaceous bed rock. Sector 17 is almost entirely cultivated.

Data collection

327 plots were studied following, as far as possible, the optimal sampling methods of Abramson (1963) and Godron (1968). Representative plots were chosen in all environments by observing the vegetation and geology of the area. If large variations of chemotype were found over short distances, a greater number of plots was sampled in that area.

In each plot, 19 factors were observed. These ecological (geographical, geological, edaphic and floristic) factors were chosen as those most likely to affect the distribution of thyme chemotypes. The observations were coded and recorded on punched cards as used by the Centre Emberger (Godron *et al.*, 1968). At each plot a sprig was taken from each of 30 thyme plants for later gas chromatographic analysis of chemotype. During the flowering season, the proportion of hermaphrodite and female plants was determined for 110 plots.

Analysis of relationships between chemotypes, associated species and ecological factors

A mutual information analysis (Godron, 1968; Guillerm, 1969; 1971; Gauthier *et al.*, 1975) revealed relations between the different ecological factors and the distribution of each species and each thyme chemotype. A second analysis was performed after transferring chemotypes to the list of dependent variables. This analysis revealed the relationships between ecological factors and chemotypes on the one hand and neighbouring plant species on the other. At the same time it was possible to draw a distribution map of the results.

Estimations of diversity

The Shannon index of diversity (Shannon, 1963; in Pielou, 1966) corresponding to entropy is calculated from the proportions p_i of the different chemotypes in the population as:

$$E = -\sum_1^n p_i \log p_i$$

where n = number of chemotypes present. It is clear that a monomorphic population gives $E = 0$ and that in polymorphic populations, *i.e.*, with more than one chemotype, $E > 0$. For a given n, E is maximised when each $p_i = 1/n$.

RESULTS

1. Distribution of chemotypes (fig. 1)

(a) *Phenolic chemotypes* The phenolic populations (T and C) are found on the limestone hills and plateaux (sectors 1, 2, 5, 6, 7, 11, 13, 14, 15,

18) and not in the depressions. They live on soils which can be grouped as regosols and fersiallitic soils (soil type numbers 0, 8, 9, 10). These are red, clayey, more or less rocky, rather shallow soils, the driest soils in the area.

Within the phenolic types there is a definite north-south division between the populations of C and T. The southern side of Pic-Saint-Loup (sectors 1 and 7) and the southern part of sector 11 are almost entirely populated with carvacrol chemotypes. In the north of the area all the uplands were occupied by populations of thymol chemotypes (sectors 5, 16, 18, 14, 15 and the north of sector 13). In the east there is a very narrow area of overlap between the populations (CT in sector 2) whereas in the west of the area the transition is broader (CT and TC in sectors 11 and 13). Though there is no evidence to suggest a selective cause for this pattern, it is possible that individuals of the carvacrol type may be more susceptible to cold than the thymol; indeed the change from C to T takes place at Pic-Saint-Loup which is considered by phyto-ecologists to divide a warmer region to the south from a colder region to the north. Moreover, additional records in other parts of the French mediterranean region favoured this interpretation: carvacrol types are found only in dry places whereas thymol types can grow in other environments.

(b) *Non-phenolic chemotypes* The area occupied by these chemotypes is clearly limited to the three depressions (sectors 8 and 17; 3 and 4; 10 and 12). The populations of TL, LT and LL are frequently found on shallow calcareous soils (soil type 2) which are damper than the rocky and fersiallitic soils of the hills. Populations of LU and UL tend to occupy soil types 1 and 4 which are wetter than the above, but not as moist as the deep dark brown calcareous soils of type 3. These type 3 soils, the dampest soils on which thyme can grow, are mostly populated with α – terpineol chemotypes (AA and AL).

This set of results shows that a fairly tight correlation exists between soil type and the chemotypic structure of the thyme population growing on it. Where there is a change of soil type, distinct differences among chemotypes can be found over a few metres. With a soil change a predictable chemotypic change occurs.

(C) *Relation to other species* The species significantly associated with different thyme populations were defined by mutual information analysis. Many species were shown to be good indicators of the single most abundant thyme chemotype (table 1). On the other hand, a small number of species was generally found to be significantly associated with pure stands or mixtures of chemotypes. This reduction could be partly due to the smaller quantity of data for these population types, but also because the environmental conditions were more selective and narrowly defined, so that the associations between the other species and chemotype are very strong.

2. Relationships between chemotype and sexual polymorphism

In the area of Saint-Martin-de-Londres, 110 populations were sampled for both chemotypes and sex-ratios. The proportion of females in the populations varies from 0·2 to 0·9. The statistical link (mutual information between the proportion of females in populations and the other observations) is displayed in table 2.

The only populations which are strongly linked with other variables are those with low proportions of females (*i.e.*, populations composed mainly of hermaphrodites). This means that the environment where hermaphrodites predominate is easier to define than the others. These populations with low proportions of females are correlated both with a high proportion of phenolic individuals and also a low degree of diversity among the chemotypes.

Table 3 gives the distribution of populations with respect to their frequency of females and chemotype. It confirms that the populations where hermaphrodites are predominant tend to be of phenolic types while populations where females are dominant tend to be of non-phenolic types.

Table 4 shows the distribution of populations with respect to the frequency of females and chemotypic diversity index. In this case, the diversity index varies from 0 to 0·7. The populations with a level of diversity higher than the median ($E > 0.35$) have with one exception an excess of females. In other words predominantly hermaphroditic populations are almost never highly polymorphic.

In table 5 a comparison is made between pure plots (monomorphic population, $E = 0$) and plots of mixed chemotype (polymorphic population, $E > 0$). The χ^2 test shows that there is no implicit association between the presence or absence of polymorphism and an excess of females. A high frequency of female plants is therefore associated with high levels of polymorphism but not with the presence of polymorphism itself.

In contrast table 6 shows that the majority of the monomorphic populations are of the phenolic

Table 1 Species significantly associated with the single most abundant or two most abundant chemotypes in a population

	Single most abundant type					Two most abundant types							
	T	C	A	L	U	TT	LL	LT	LU	LA	UL	AA	AL
Pistacia terebinthus	+	+											
Quercus ilex	+	+				+							
Phillyrea latifolia	+												
Juniperus oxycedrus	+					+		+					
Smilax aspera	+					+							
Acer monspessulanum	+												
Quercus coccifera	+												
Euphorbia characias	+												
Cephalaria leucantha	+												
Brachypodium ramosum	+												
Helleborus foetidus	+												
Juniperus phoenicea	+												
Antirrhinum majus	+												
Psoralea bituminosa	+												
Quercus lanuginosa		+											
Prunus mahaleb		+											
Galeopsis ladanum		+											
Ribes uva crispa		+											
Potentilla verna			+	+									+
Globularia vulgaris			+	+									
Koeleria vallesiaca			+	+									
Fumana coridifolia			+	+									+
Aphyllanthes monspeliensis			+	+									
Bupleurum nigidum			+	+									
Carex halleriana			+	+									
Thesium divaricatum			+	+								+	
Scorzonera hirsuta			+	+									
Euphorbia nicacensis			+	+									
Asperula cyranchica			+	+						+			
Sideritis scordioides			+					+				+	
Teucrium polium			+										+
Linum salsoloides			+									+	
Carduncellus mitissimus			+										+
Helianthemum canun			+									+	
Lithospermum fruticosum			+										+
Genista scorpius			+										
Coris monspeliensis			+										
Coronilla minima			+										
Linum campanulatum			+										+
Argyrolobium linnaeanum				+									
Lavandula latifolia				+									
Eryngium campestre				+				+					
Avena bromoides				+									
Ononis minutissima				+									
Leuzea conifera				+									
Bromus erectus				+									
Teucrium chamaedrys				+									
Dianthus caryophyllus				+									
Trifolium angustifolium				+									
Artemisia campestris				+	+								
Thymus serpyllum					+								
Brachypodium pinnatum					+								
Amelanchier rotundifolia					+								
Hedera helix					+								
Viola alba					+								
Asplenium ruta-muraria					+								
Sedum nicaense						+							
Satureia montana						+							
Andropogon ischaemum						+							
Sideritis romana							+						
Crucianella angustifolia							+						
Filago germanica							+						
Rosmarinus officianalis									+				
Andropogon gryllus										+			
Carex glauca											+		

The first letter indicates the most abundant chemotype, the second indicates the next most abundant. Two identical letters indicate a pure or almost pure stand IC, TL, CC, CT, CL and GL are omitted because too few samples of these population types were available to define clearly the other species sympatric with these populations.

Table 2 Observations related with the proportion of females in thyme populations

Strength of Relationship (MI/FE)*	Proportion of females		
	Low 0–50%	Medium 50–70%	High >70%
High (>4%)	Bedrock: hard limestone Xeric environments Phenol types Most dominant species: *Quercus ilex* and *Thymus vulgaris* Frequency of dominant chemotype >0·70 (low polymorphism)		
Medium (2–4%)	Shallow soil Trees T and C chemotypes Low proportion of fine soil	Relative paucity of T or TC populations Most dominant species: *Genista scorpius* Frequency of dominant chemotype: 0·50–0·70 (polymorphic population) Soil free from stones	Most dominant species: *Aphyllantes monspeliensis* *Rosmarinus officinalis* *Quercus lanuginosa*

* MI/FE; mutual information index (Godron, 1968).

type whereas the majority of the polymorphic populations are non-phenolic. Thus, there is a strong correlation between the most prevalent chemotype and the presence of polymorphism.

The other ecological characteristics which are linked with a low proportion of females (table 2) show that these populations are found in the most stable environments where hard limestone prevents cultivation and so allows the presence of trees, notably *Quercus ilex*. This environment is very xeric. In contrast, the populations with medium and high proportions of females tend to grow where there are shrubs (*Genista scorpius*, *Rosmarinus officinalis*) characteristic of disturbed environments, or grass and trees characteristic of mesic environments (*Aphylantes monspeliensis*; *Quercus lanuginosa*).

Table 3 Contingency table showing the number of plots according to the proportion of females and prevalent chemical type (>50%)

Chemical type	Proportion of females	
	≤50%	>50%
Phenolic	24	28
Non-phenolic	11	47

$P(\chi_1^2 > 9·3) < 0·01$

Table 4 Contingency table showing the number of plots according to the proportion of females and chemotypic diversity

Diversity index	Proportion of females	
	≤50%	>50%
E < 0·35	34	59
E > 0·35	1	16

$E = -\sum p_i \log p_i$ $P(\chi_1^2 > 6·2) < 0·02$

Table 5 Contingency table showing the number of plots according to the proportion of females and the presence or absence of chemotypic diversity

Diversity index	Proportion of females	
	≤50%	>50%
Monomorphic (E = 0)	15	26
Polymorphic (E > 0)	20	49

$P(\chi_1^2 > 0·7) > 0·40$.

Table 6 Contingency table showing the number of plots according to the population type and the presence or absence of chemotypic diversity

Diversity index	Population type	
	Phenolic	Non-phenolic
Monomorphic (E = 0)	54	37
Polymorphic (E > 0)	80	156

$P(\chi_1^2 > 17·5) < 0·001$.

DISCUSSION

Thymus vulgaris is extremely common in the French mediterranean region, characterising both the region and its climate. It figures among 29 out of 149 major phyto-ecological groups in the region (Braun-Blanquet, 1952). It is found in many environments without particularly characterising any. This study suggests that the genetic diversity of thyme gives it much plasticity, since the distribution of intraspecific variability, here chemotypes, appears to be very strictly defined by environment. The selective forces at work in any one environment favour particular chemotypes or combinations.

The relation between soil type, associated species and thyme chemotype found in this area cannot be considered to be universally applicable over the whole area of distribution of the species. For example, the U chemotype is associated with a fairly deep soil in the area sampled, but with a shallow-rocky soil on a mountain at 500 to 900 m altitude a few kilometres to the north. Thus these shallow rocky soils are occupied by phenolic populations in the area studied, whereas at much higher altitudes U populations abound. Therefore one must conclude that the soil type acts only indirectly on the chemotype distribution. The real factor (if any) influencing the distribution of these chemotypes could be, in fact, the moisture (itself depending on the soil type). Even in this case, the moisture could itself act indirectly by changing the abundance of predators (or competitors) for instance.

The following interpretation is proposed for the mechanism of ecological selection of the phenotypes studied. In stable and xeric environments thyme is in its "home" environment. There it expresses the most chemically elaborate chemotypes, T or C. This environment is almost constant, very few disturbances arise and the few species which are able to grow there have slow growth rates and are almost always the same. This could be related to the fact that the thyme populations growing there were predominantly hermaphrodite (able to self-fertilise) and largely homogeneous in regard to chemotype. The highly successful phenolic (T and C) phenotypes can self-fertilise and produce more of the same successful type. Vernet, Gouyon and Valdeyron (in press) showed that when T plants are selfed they produce only T progeny. When C plants are selfed they produce either C progeny or T and C according to their genotype. Thus clearly correlation occur between stable environment and low genetic diversity.

In more "difficult" environments, where disturbance occurs or where the greater amount of moisture results in an increasing intensity of interspecific competition, selection may be greater for genetic diversity. These environments are much more heterogeneous and not as stable as the previous ones and thus having a greater genetic heterozygosity may be advantageous for the individual itself (Gouyon and Vernet, 1982) or its progeny (Valdeyron *et al.*, 1973).

Thus, in these environments, females can be selected for and promote a high genetic diversity because of their obligate outcrossing. Another way in which genetic diversity is achieved is by the nature of the genetic control of chemotype. Non-phenolic chemotypes, which are favoured in this environment, are capable of producing a wide range of chemotypes among their progeny (Vernet *et al.*, in press). This is because G, A, U and L chemotypes carry dominant genes which prevent the production of phenols. As a result these chemotypes, when heterozygous, can produce phenolic types among their progeny by the combination of two recessive genes. In fact a self-fertilised G individual, heterozygous at all loci, is theoretically able to produce all possible chemotypes among its progeny. Thus phenolic genes are latent in non-phenolic populations. Even if the phenolic individuals are strongly selected against over some years or across some distance they may appear again when conditions change. On the contrary, phenolic populations remain homogeneous over several kilometres since the dominant non-phenolic genes are eliminated immediately.

There is another factor which could explain why the non-phenolic chemotypes are better competitors in a more highly competitive environment. The very production of monoterpenes requires energy, and probably more energy is required to produce thymol and carvacrol than α-terpineol and geraniol. According to Trenbath and Morrow (1978), the energy used to produce the aromatic compounds in *Eucalyptus*, which represent 15 per cent of the dry weight of the leaf, was 34 per cent of the total energy used by the plant for growth. Although we have no figures available, one might assume that the significantly smaller quantity of energy used by thyme for geraniol synthesis than for thymol synthesis enables the G plants to grow faster and to be more competitive than a T plant. However, the disadvantage in energy efficiency of the phenolic types must be counterbalanced in other situations, otherwise pure stands of phenolic types would not exist. For example, the study by Gouyon *et al* (1983) supports the hypothesis that

the terpene produced can be related to the level of predation by slugs. Thus, the interruption of the chain of biosynthesis may be selectively advantageous where there is little predation, or at least when predation is not a crucial problem for the plant. It is nevertheless possible that physiological constraints could play a direct role in the distribution of polymorphism.

CONCLUSION

The chemical polymorphism in *Thymus* demonstrates different aspects of the way populations become adapted to their environment.

—Some chemotypes are favoured in the "home" area of the species while others are found in more marginal or disturbed situations. The reasons why certain chemotypes have a selective advantage are being investigated using predation and physiological experiments.

—The extent to which genetic diversity in oils and sexual polymorphism are promoted seems to differ according to the environment. This diversity can be related to the sex-ratio which affects the reproductive strategy. In some populations individuals are now mapped and are being followed from year to year to investigate the mechanism linking sex-ratio with chemotype diversity.

—Changes in population composition over very short distances are possible because the low migration rate (see introduction) means that the effects of selection persist.

From tables 2, 5 and 6, it is possible to assume that this strategy of low dispersal allows a precise adaptation of the population to its environment, but increases the homogeneity of the population and thus probably decreases its adaptability. These results also indicate that when changes occur a more open reproductive system given by the presence of female individuals, which are cross pollinated and produce more seeds (Dommée *et al.*, 1978; Couvet, 1984), can be selected with the result that the genetic diversity of the population is increased. The problem of the balance between the need for homogeneity, linked to adaptation to precise conditions, and the selection for the heterogeneity necessary to maintain a certain adaptability, has important implications in ecology and in agronomy and thyme provides a good example of the way such a compromise can be produced by natural selection in different and sometimes opposite ways.

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