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CHRONICA BOTANICA

NEW SERIES OF PLANT SCIENCE BOOKS

Consulting Editor, Frans Verdoorn

No. 33

PLANT LIFE OF PALESTINE

Israel and Jordan

MICHAEL ZOHARY

PROFESSOR OF BOTANY
THE HEBREW UNIVERSITY OF JERUSALEM

THE RONALD PRESS COMPANY · NEW YORK

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Library of Congress Catalog Card Number: 61–15614
PRINTED IN THE UNITED STATES OF AMERICA

Preface

Botanical explorations in the Near East have considerably furthered our knowledge of the flora of this part of the world. Surprisingly, however, scant attention has been paid to Near Eastern ecology and vegetation. This book gives a factual account of, and an insight into, the static and dynamic problems concerning Palestine's flora and vegetation, problems which are shared by neighboring lands. Palestine, as considered here, comprises Israel and Jordan, plus the Gaza Strip. The name has been used for generations for this historico-geographical unit characterized by many biogeographical features. Although small in area, Palestine is marked by a diversity of climatic, topographic, and edaphic features, and its comparatively rich flora and vegetation range from wood formations to sparse herbaceous desert communities.

There is a discussion of the ecological factors responsible for the diversity of Palestine's vegetation types and a review of its soil varieties and climatic conditions. To reveal the phytogeographical affinities, an analysis is made of the geographical distribution of more than two thousand native species of vascular plants. According to the ranges of these species, thus established, Palestine is subdivided into biogeographical areas, each of which is characterized not only by its flora and plant communities but also by its agricultural features. Considerable stress is laid on the arboreal vegetation, past and present. Man's activities through the millennia have largely influenced the structure of the vegetation but have not succeeded in obliterating its peculiar characteristics. This continuing relationship is stressed in the book, which also enumerates the native plants used by man for various purposes.

Increasing interest is evident in the problems and potentials of arid land development, and it is the author's hope that the information on Palestine's flora and vegetation, brought together in this volume, will be of help in evaluating its agricultural or other land utilization potentialities. The material is based on observational and experimental data collected during the past three decades, some of which has been published previously in various periodicals. For

many of the data, the author is indebted to his colleagues and co-workers, with whom he has spent many hard and happy days in field work. In particular, cordial thanks are extended to Dr. G. Orshan, Dr. D. Zohary, Dr. Naomi Feinbrun, Y. Waisel, J. De Angelis, and A. Grizi. Their help has been indispensable. To Mrs. Irene Gruenberg-Fertig, Augusta Horowitz, and Sybil Broide go his thanks for their aid in preparing the manuscript.

MICHAEL ZOHARY

Jerusalem, Israel

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PLANT LIFE OF PALESTINE

1

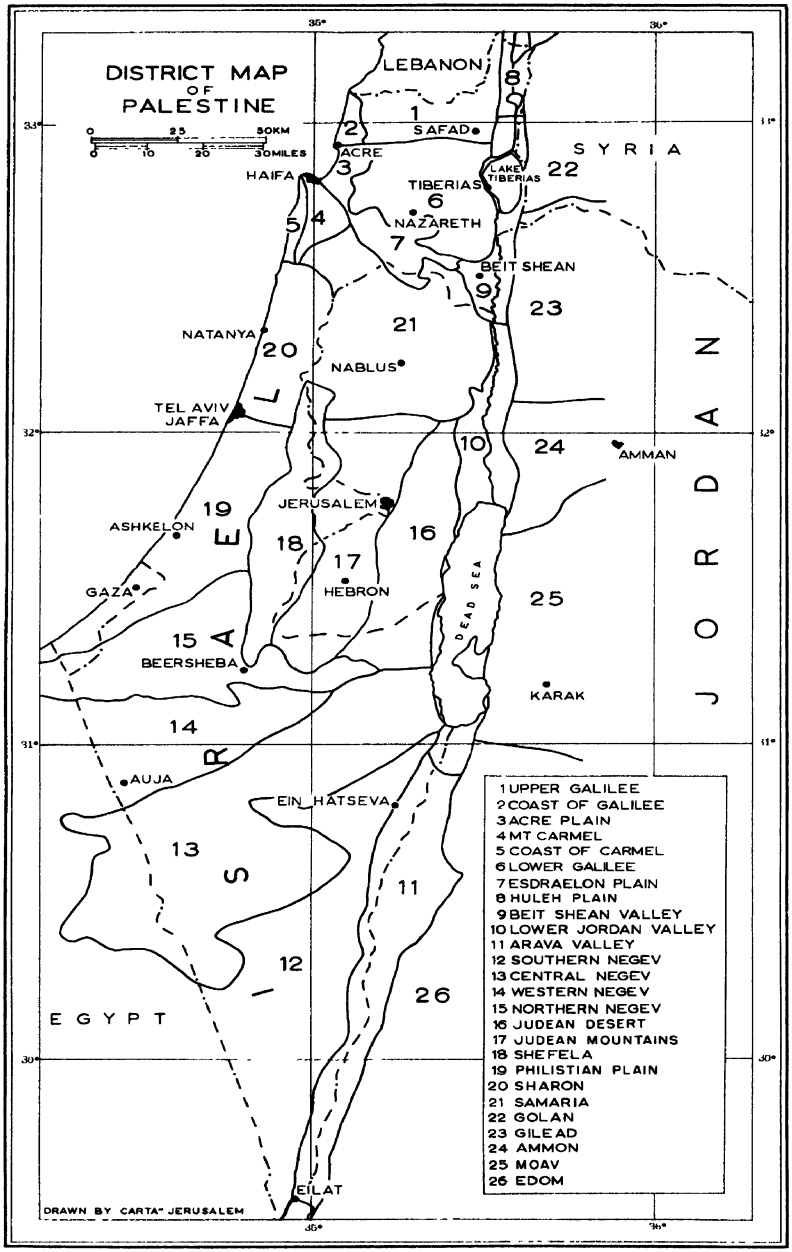
Topography and Soils

Topography

Palestine is here considered as the historical-geographical area now comprising Israel, Jordan, and a small part of the United Arab Republic. It occupies the southeastern corner of the Mediterranean Basin and borders to the east and south on the steppes and deserts of the Near East, which are partly included within its boundaries. It is an area of striking contrasts in its topography and climate. Its highest mountain peak, in Edom (Transjordan), rises to 1700 m. above sea level; its lowest depression, in the Dead Sea region, falls to 396 m. below sea level. Its northern districts enjoy a typical Mediterranean climate while its southern parts are dreary deserts. The total land area of Palestine, including both sides of the Jordan River, is estimated at about 117,000 sq. km.; of this, Cisjordan comprises some 27,000 sq. km. only. None of its area boundaries coincides with biogeographical or ethnic demarcation lines.

The Topographic Belts. Palestine has four longitudinal topographic belts: the coastal plain, the western mountain region, the Jordan Valley with its southern continuation to the Gulf of Aqaba, and the Transjordan Plateau. These belts are fairly well marked by differences in their geomorphologic features, their climatic and edaphic conditions, and their plant life.

The coastal plain broadens toward the south and attains its maximum width of approximately 60 km. in the Negev. In its greater part it is subject to a true Mediterranean climate and harbors a flora and vegetation peculiar to that climate. It is here that the main citrus groves are centered. Ever since Biblical times this plain has been transversally subdivided into four districts (Map 1): the Negev Plain (in the south), and the Philistia, Sharon, and Acre plains (in the north). With a gradual deterioration of climatic conditions


DISTRICT MAP
OF
PALESTINE
0 25 50KM
0 10 20 30MILES
LEBANON
SYRIA
JORDAN
SAFAD
ACRE
HAIFA
TIBERIAS
LAKE TIBERIAS
NAZARETH
BEIT SHEAN
NATANYA
NABLUS
TEL AVIV JAFFA
JERUSALEM
AMMAN
ASHKELON
GAZA
HEBRON
DEAD SEA
BEERSHEBA
KARAK
AUJA
EIN HATSEVA
EILAT
EGYPT
SHEFELA
NEGEV
1 UPPER GALILEE
2 COAST OF GALILEE
3 ACRE PLAIN
4 MT CARMEL
5 COAST OF CARMEL
6 LOWER GALILEE
7 ESDRAELON PLAIN
8 HULEH PLAIN
9 BEIT SHEAN VALLEY
10 LOWER JORDAN VALLEY
11 ARAVA VALLEY
12 SOUTHERN NEGEV
13 CENTRAL NEGEV
14 WESTERN NEGEV
15 NORTHERN NEGEV
16 JUDEAN DESERT
17 JUDEAN MOUNTAINS
18 SHEFELA
19 PHILISTIAN PLAIN
20 SHARON
21 SAMARIA
22 GOLAN
23 GILEAD
24 AMMON
25 MOAV
26 EDOM
DRAWN BY CARTA* JERUSALEM

Map 1.

from north to south, each of these districts exhibits certain biogeographical features of its own. Edaphically, one can distinguish four well-defined longitudinal zones in the coastal plain: the zone of mobile sand dunes, that of interrupted calcareous-sandstone hills, the belt of sandy clays ("red sands"), and the zone of alluvial-colluvial heavy soils (cf. Map 2). Impeded in their way to the sea by dune and sandstone ridges, some of the latitudinal watercourses which cross the coastal plain have turned considerable land stretches into swamps and marshes. These have been dried up only recently and are now being utilized for agriculture.

The western mountain region constitutes a belt of considerable width. It extends from the southern foot of Mount Lebanon to the Desert of Sinai and reaches its peak (1208 m.) in the north (Jebel Jarmak in upper Galilee). While the western, gently sloping side of these mountain ranges has a Mediterranean climate and vegetation, the abrupt eastern slopes, which face the Jordan Valley, are mostly desert or semidesert. Of the latitudinal valleys that interrupt the continuity of the western mountain region, the largest are the Esdraelon Plain in the north and the Plain of Beersheba in the south. The Negev, Judea, Samaria, and Galilee (Map 1) are the four main districts into which that region is commonly divided. The Negev is the largest and most desolate part of Palestine. As a whole it is an unsown desert with a rough topography. The other districts, though fairly well distinguishable biogeographically, share many features. The rocky, heavily eroded landscape, with its many ravines and shallow valleys, is common to all three. The so-called Judean Desert occupies the eastern parts of Judea and Samaria.

The Jordan Valley, the lowest depression of the earth's surface, is the most significant feature of Palestine's topography. It is part of a rift valley, which extends from the Orontes River in Syria to the Gulf of Aqaba and continues further into the Red Sea and the continent of Africa. In Palestine it ranges in elevation from −396 m. in the Dead Sea region to +200 m. in the Dan Valley (Huleh Plain); mountains border it on both sides. Its southern part comprises deserts, salines and tropical oases, while in its northern part there are swamps and fertile land stretches situated within a Mediterranean wood climax area.

The Transjordan Plateau is higher in its northern and southern edges than in its central part. To the east this plateau merges gradually into the Syrian Desert. Its steep western escarpments are crossed by a series of latitudinal rivers, which empty into the Jordan Valley and the Dead Sea and divide the comparatively narrow western strip of the plateau into transversal districts known since Biblical times as

Edom, Moav, Ammon, Gilead, and Golan (Map 1). Edom, the southernmost district of this plateau, is marked by vast sand deserts that border on the country's highest mountain ranges, which reach a height of 1700 m. These afford conditions for the extension of Mediterranean woods as far south as the latitude of Cairo.

Soils

The occurrence of so great a number of plant communities in Palestine, even within climatically uniform zones, is due largely to the great diversity of prevailing edaphic conditions. Among the obvious edaphic factors bearing on plant life, highest significance must be ascribed to soil properties responsible for moisture relations and accumulation of injurious salts.

Soil Development. Continuous erosion, brought about by climate, topography, and man, impedes the development of soil profiles. Removal of upper soil horizons from the hills and mountains and their accumulation in the lowlands perpetually rejuvenates the soil profile. Predominance of physical weathering processes in the desert and semidesert areas keeps soil development in its early stages, even where topography is smooth. Typical *A-B-C* profiles are never found here—not even in virgin soils beneath a cover of Mediterranean vegetation. Instead, so-called *A-C* or *C* profiles are most characteristic. There is, however, a marked difference between Mediterranean and desert soils as regards their ultimate stages of development. In the former, the soil profile, when formed under an arboreal vegetation cover, has a humiferous topsoil layer, whereas under conditions of the open desert vegetation a humiferous layer is never formed.

From the pedogenetic point of view, the soils of Palestine may thus be subdivided into the following categories: residual mountain soils with *A-C* or *C* profiles, alluvial-colluvial loams of the great agricultural plains and valleys, aeolic soils (e.g., loess and sands), and hydromorphous soils (swamps and marshes).

Parent Material. The most abundant surface formation of the country belongs to the Cretaceous period. The so-called Nubian sandstone layers of the Lower Cretaceous occupy considerable areas in Edom and lesser ones in Moav, Gilead, and the Arava Valley. This rock produces a sandy soil and interior desert sand dunes. However, it is the rocks of the Upper Cretaceous layers which are the most important soil source both in Cis- and Transjordan. The Cenomanian and the overlying Turonian hard rocks are the main parent material of the terra rossa. Another parent rock is the Santonian

(Lower Senonian) limestone, which weathers into terra rossa even under arid conditions. The soft rocks of the Middle and Upper Senonian yield the gray and whitish-gray soils that are abundant in steppes and deserts and are also not uncommon in the Mediterranean portion of Palestine. In the latter they tend to develop at times into rendzina and similar soil types.

The Eocene strata are almost the only well developed and widespread rocks of the Tertiary. The hard rocks of these strata may produce terra rossa, whereas the more common soft chalks and marls weather into bright or dark rendzinas. Quaternary formations are widely distributed all over Palestine. Large stretches of the Jordan Valley consist of the so-called Lissan marls—a fine-layered deposit of the diluvial, brackish, ancient "Jordan Sea." The coastal dunes and the so-called "older dunes," or "kurkar," and "red sands" of the coastal plain, the vast expanses of hammada, and the loess deposits of the steppes and deserts are all products of the late Tertiary and Quaternary eras. During the latter period alluvial and colluvial loams accumulated in the plains and lowlands; this led to the formation of the most fertile soils of Palestine.

Basalts, which occupy certain areas in the northeast, weather into a brown, heavy soil. Less important are the igneous rocks, such as granites, gneisses, and porphyries of southern Palestine. Under desert conditions they give rise to the formation of barren sands and sand dunes.

Soil Distribution. Without minimizing the part played by climate upon the genesis of soils, there is evidence for the equal importance of topography and the nature of parent rock as factors in the make-up and distribution of soil varieties here, as in other arid regions. For example, terra rossa is associated in Palestine with hard limestone, white-grayish soil with soft chalks, marls, etc. Sandstone and basalt rocks never weather into terra rossa, not even under typical Mediterranean climatic conditions. This shows that different soil types may occur under the same climatic conditions, and that climate is unable to efface those peculiarities of the soil which have their origin in the constitution and nature of the parent rock. A glance at the accompanying soil map (Map 2) shows that terra rossa, rendzina and rendzina-like soils, gray-brown alluvial-colluvial loams, basalt soils, and light sandy soils occur within the Mediterranean territory, while the steppe and desert parts of the country comprise white-grayish steppe soil, loess, different varieties of hammada, salines, and sands.

Many of the pedological data given here are taken from Menchikovsky (1927, 1938), Puffeles (1936, 1937), Ravikovitch (1935, 1946,

GEOBOTANICAL
SOIL MAP
OF
PALESTINE
BY
M. ZOHARY
SCALE
50 KM.
30 MILES
LEGEND
1 TERRA ROSSA
2 DARK RENDZINA
3 LIGHT COLOURED RENDZINAS
4 MOSAIC OF N°1 AND N° 3
5 BASALT SOILS
6 SAND DUNES
7 SURSAR AND SANDY CLAY SOILS
8 ALLUVIAL SOILS
9 CALCAREOUS STEPPE SOILS
10 LISSAN MARLS (NON SALINE)
11 GALG STEPPE SOILS LOESSY IN DEPRESSIONS
12 LOESS
13 SANDY LOESS
14 HAMADA LIKE ROCKY SURFACE
15 SALINE SOILS
16 INTERIOR SANDSTONE AND MARLY SOILS
17 MOSAIC OF N°9 AND N°12
18 TRANSPORTED TERRA ROSSA AND RENDZINAS
19 HAMMADA PLAINS
20 SOLONCHAK WITH CLAY AND SILT LOESS IN DEPRESSIONS
REFERENCE
M ZOHARY M FEBRUR 1941
M ZOHARY M FEBRUR 1943
M ZOHARY D DESHNESKY 1943
M ZOHARY 1939-1943
D ZOHARY 1945-1946
LEBANON
SYRIA
EGYPT
METULA
HANITA
ACRE
HAIFA
SAFAD
TIBERIAS
LAKE TIBERIAS
NAZARETH
ATLITH
DALIA
AFULA
ZIKHRON YAAQOV
JENIN
HADERA
NATHANYA
TULKARM
TUBAS
QALQILYA
NABLUS
TEL AVIV
JAFFA
RIDA
REHOVOT
RAMALLA
JERICHO
JERUSALEM
BETHLEHEM
BEIT GUVRIN
HEBRON
AMMAN
ASHKELON
GAZA
RAFA
BEERSHEBA
SEDOM
SEDE BOQER
AUJA
KARAK
TAFILA
PETRA
MAAN
WADI
ARABA
DEAD SEA

Map 2.

1950), Ravikovitch and Bidner (1937), Reifenberg (1927, 1929, 1938), Reifenberg and Adler (1934), Reifenberg and Moshicky (1941), and others. Other analytical data have been obtained through the author's own investigation.

Soil * Varieties

The Terra Rossa Series. † Terra rossa (No. 1) is the most characteristic soil unit of Mediterranean Palestine. It is derived from hard limestone and dolomites of the Upper Cretaceous (mainly the Cenomanian, Turonian, and Santonian), as well as from certain Eocene rocks. The chemical and physical compositions of terra rossa have been the subject of pedologic studies (Reifenberg, 1929) and need not be taken up in detail here. It must be pointed out, however, that terra rossa comprises a number of varieties which often supersede each other and form a genetic series in correlation with the successional stages of vegetation.

There is a marked difference between residual (oropedic) and transported terra rossa. The former reflects the virgin state of this soil series and its profile development is dependent upon vegetation. The transported soil that accumulates in lowlands and in intermountain valleys is very much under the influence of prevailing water conditions, and its physical properties change to such an extent as to be best classed within the alluvial-colluvial soil series.

What has been examined hitherto and described as terra rossa by most authorities represents only a degraded stage of this series which has been preserved under open or devastated vegetation, on eroded slopes, or on land under cultivation. Where there is a vegetation of primary forest or maquis, on the other hand, a more or less well-differentiated *A*-horizon is found overlying the *C*-horizon of the weathering rock. This *A*-horizon often consists of a layer of organic debris above a richly humiferous subhorizon (A_0) which, in turn, merges gradually into the brown to dark brown mineral subsoil (A_1). Thus, without an accumulative horizon this *A-C* soil supports forest or maquis of *Quercus calliprinos–Pistacia palaestina.* The destruction of these communities by man brings about the removal of the humiferous layer. At this stage the soil may be occupied by dwarf shrub communities, leading again to the woody climax. If, on the other hand, the soil is exposed to further denudation, it becomes

* The term "soil" is used in a broad sense here. It includes unconsolidated geological strata and sometimes even rocky ground, as long as this supports vegetation. The different soils mentioned do not always represent conventional pedologic types but edaphic units characterized by their particular vegetation.

† The term "series" as used here applies to groups of varieties of common origin. The number in parentheses corresponds to that in the legend of the soil map (Map 2).

skeletic and rocky, and its vegetation consists only of sparse shrubs and lithophytes.

Terra rossa is a fertile soil, on the whole. Its $CaCO_3$ content ranges from 15 to 40 per cent. It contains a fairly high proportion of silt and clay and is fairly rich in sesquioxides. It has a high field capacity, but also a rather high wilting coefficient. Although it is generally very shallow, this soil supports most of the native trees and shrubs, as well as many cultivated trees. These send their roots into the crevices and earth pouches between the rocks, where available moisture is present throughout the year. On the other hand, its shallow profile and rough topography makes the entire mountainous terra rossa belt unfit for cultivation with modern implements, so that agriculture here is limited to narrow terraces.

The Rendzina Series. Along with typical terra rossa, and under identical climatic conditions, there occurs a series of gray to grayish-white soils that is classed as rendzina. The parent rocks of this series are soft calcareous formations of the Upper Cretaceous and Eocene, including chalks, soft limestones, marls, and "nari" (amorphous chalk crust covering the rock). The humiferous topsoil, which is formed in the advanced stages above the gray subsoil, is a common feature of the entire series. Soil areas with mature profiles are rare, however, unless preserved under an arboreal climax vegetation. Where vegetation has been destroyed, the humiferous layer has vanished, and in extreme cases only *C*-horizon remains. Smoother topography and the soft underlying rock material have made this soil more easily accessible to cultivation than the terra rossa. In consequence, its vegetation has suffered much more destruction than that of the red soils. The following are a few of the common varieties of the local rendzina.

Dark Rendzina (No. 2). This is derived from the calcareous rocks of the Lower and Middle Eocene and is confined to northwestern Samaria and southwestern lower Galilee. When under a forest cover, the profile consists of a thin layer of raw humus, gradually merging into a dark, gray to black humiferous *A*-horizon, sometimes devoid of $CaCO_3$. A certain type of the Quercetum ithaburensis forest is most characteristic of this variety.

Light-colored Rendzinas (No. 3). The main varieties of this group are derived chiefly from soft Senonian chalks, "nari," and Cenomanian marls. In its natural state, the profile consists of a thin humus layer and of a gray, slightly humiferous and highly calcareous A_1-subhorizon above the soft parent rock. Light-colored rendzinas occur most commonly in the northern and central part of Mediter-

ranean Palestine (e.g., upper Galilee, Mount Carmel, Samaria, and the northern part of the Judean Mountains). The *Pinus halepensis–Hypericum serpyllifolium* association characterizes this soil.

GRAYISH-BROWN RENDZINA. This is derived from compact Upper Eocene rocks and is confined to the southwestern Judean Mountains. It has a topsoil which is fairly rich in organic matter and a calcareous subsoil. Its composition and properties are as yet inadequately known, but from its appearance and vegetation it seems to be somewhat intermediate between rendzina and terra rossa. The immense stretches of grayish-brown, alluvial soil ("salaga") of the Philistian Plain are deposits of this type of soil.

Basalt Soils (No. 5). These soils occur only in northeastern Palestine. They are alkaline and rather variable in their composition and properties; their lime content ranges between 5 and 15 per cent. Their soil profile is very shallow and when inhabited by arboreal vegetation, it consists of a thin humus layer covering a dark brown *A*-horizon, which gradually merges into the parent material. The latter is made up mostly of great angular boulders or, occasionally, of less consolidated gritty particles. Under open vegetation or under arable conditions basalt soils are marked by a characteristic chocolate-brown tint and by a low organic matter content. Though of heavy texture, these soils are apt to dry out rapidly. The greater part of the Palestinian basalt area adjoins the Irano-Turanian territory, or lies within its boundaries, and is often characterized by semisteppe vegetation. Even under conditions of Mediterranean climate it rarely supports a typical Mediterranean maquis.

Sandy and Sandy-Calcareous Series. The sandy and sandy-calcareous soils of the Mediterranean coastal plain constitute a genetic series. They are aeolic in origin, and some of them have undergone pedogenetic changes resulting in decalcification, hardpan formation, etc. The main units belonging to this series are: sand dunes; calcareous sandstone soil, locally termed kurkar; and red sandy clay.

SAND DUNES (No. 6). The sand dunes of Mediterranean Palestine occupy a discontinuous belt along the sea coast. They are composed mainly of silica grains intermingled with hornblende, mica, felspar, etc. With the exception of the Acre Plain, which has a flat sandy shore, most of Palestine's coast line is elevated and steep. It is built of sandy clay layers, stratified between friable calcareous sandstone. The sandy material of the high coast is continuously blown inland by onshore winds and piles up in lofty dunes, 10–50 m. in height, at some distance from the coast line. On flat shores the

dunes are lower, close to the shore, and consist of two belts: the spray zone affected by windborne seawater drops and the shifting dune zone. Each belt is characterized by a series of plant communities which will be discussed in a later chapter South of Gaza, in the Negev and Sinai, the belt of the Mediterranean coastal dunes widens considerably (Fig. 1).

Fig. 1. Sterile sand dunes on the southern border of the western Negev.

Apart from the maritime dunes, there are stretches of interior desert sands and dunes derived from local Neogene sandstone in the Mamshit (Kurnub) region (eastern Negev) or Nubian sandstone and igneous rocks in Edom and the Arava Valley. Although subject to an extremely arid climate with an annual precipitation of 50–100 mm., these sand areas are comparatively rich in vegetation

KURKAR, OR CALCAREOUS SANDSTONE SOIL (No. 7). On the interrupted hill ridges along the coastal plain a sandstone has been formed from diagenetically hardened dunes, the sand grains having been cemented by lime solutions. In several places this terrestrial sandstone overlies a compact red-brown, decalcified sandy loam, which, in its turn, is deposited above deep-seated calcareous sandstone strata. At present the sandstone weathers into a coarse sand soil, while the compact sandy loam produces sandy clay.

The particular plant communities of the kurkar hills vary from south to north with the increasing amount of annual rainfall.

SANDY CLAY (RED SANDS) (No. 7). This is the most fertile of the light soils of the coastal plain. It is derived from the compact sandy

loams that occur above and below layers of kurkar. This belt attains its maximum width between Rehovot and Pardess Hanna in the Sharon Plain. It is a light red soil of great depth, which consists mainly of silica sand and sesquioxides and is entirely or almost entirely lacking in lime. As in the case of the dunes and kurkar, profile development is feeble, except for the sporadic occurrence of hardpan where sesquioxides have accumulated. Its reaction is neutral, or nearly so, and its moisture retention capacity is low. This soil lends itself to the growing of citrus and of the more intensively irrigated crops in Israel. Its climax vegetation (from the Yarkon River northwards) is a kind of QUERCETUM ITHABURENSIS.

Alluvial Soil Series (No. 8). This series comprises soils which have been transported through erosion from the uplands into the plains, flood valleys, low terraces, and intermountain valleys. One can distinguish between different varieties according to origin, way of redeposition, and drainage. Among the features common to all of them are heavy texture, high moisture-holding capacity, a high proportion of silt-clay fraction, as well as a high wilting coefficient. Most of the alluvial soils occur within the Mediterranean territory, where they form a fairly broad belt between the light soils and the foothills, with adjoining strips along the latitudinal watercourses. Fairly large extents of this soil occur in the Esdraelon Plain, the Beit Netufa Valley (upper Galilee) and other valleys of Galilee and Samaria, and in the Jordan Valley.

Non-hydromorphous varieties of the alluvial soil series are Palestine's most valuable lands, and have been under cultivation since time immemorial. Their original vegetation has been almost completely effaced long ago and secondary vegetation consisting of segetal plant communities has taken its place.

On river banks and swamps heavy alluvial loams support a typical hydrophilous vegetation which is arranged in easily distinguishable zones.

The oases soils of the lower and middle Jordan Valley, which also belong to this series, have for the most part been transported by water currents from adjacent and distant mountains and are, therefore, very different in origin from the surrounding desert and saline soils. Free from sodium salts, sufficiently moist, and subject to comparatively high winter temperatures, these soils support a tropical vegetation.

The peat soil of the Huleh swamps, too, may be included within this series. This is an alkaline peat formed on a seasonally flooded bog. It is extraordinarily rich in hydrophilous plant communities.

These are arranged zonally around the *Cyperus papyrus–Polygonum acuminatum* association, which covers the larger part of the area. Most of this swamp has recently been drained and turned into agricultural land.

Gray Calcareous Steppe Soil (No. 9). This type occurs throughout the Irano-Turanian territory of Palestine and is most characteristic of the Judean Desert and the near Negev. It is derived mostly from soft chalk and limestone of the Senonian and Eocenian formations and differs from Mediterranean rendzinas in lacking a humiferous layer, even in its primary state. *C* or immature *A-C* profiles are very characteristic of this soil. It is generally poor in colloidal and nutritive matter, extraordinarily rich in $CaCO_3$ (60–90 per cent), and is fairly dry but never saline or gypseous. Its climax vegetation consists of open shrub and dwarf shrub communities.

In the southern and southeastern portions of the Judean Desert, and partly also in the Negev, there are areas where the gray steppe soil of the hills and plateaus alternates with loess-like soil accumulated in depressions and wadi beds. These depressions are frequently cultivated and support a vegetation similar to that of the loess to be described below. Since these areas are very striking in appearance, we have marked them as a particular unit (No. 11).

Lissan Marls Soil (Non-saline, No. 10) This soil is a derivative of calcareous, delicately stratified marls, containing among their constituent materials a considerable proportion of gypsum. At one time these marl strata formed the bottom of the diluvial brackish "Jordan Sea," which extended from the Arava Valley to Lake Tiberias. It is a white-grayish soil with a high percentage of lime. Whereas in the southern part of this area the soil is strongly saline, in the northern part it has been leached of its injurious salts. The larger part of this soil area is at present under cultivation (Beit Shean Valley), and its segetal vegetation is characterized by a particular variant of the *Prosopis farcta* community. The southern portion of this Lissan marl basin (lower Jordan Valley and northern Arava Valley) is classed within the saline soils.

Loess Series (Nos. 12, 13). These soils are chiefly confined to the Irano-Turanian parts of the Negev and Transjordan (Plain of Beersheba, Edom, etc.). The local loess is a soil transported mainly by wind storms from southern and eastern plantless desert areas of sands and hammadas. It is deposited mostly in plains and intermountain valleys. The calcareous rocks of the hills adjacent to the loess area may under some circumstances also take part in supplying the soil material.

Neither the loess of Palestine (No. 12) nor that of North Africa and Southwest Asia is identical with that of northern humid regions. It is a fine-grained soil with a medium clay/silt ratio and a high proportion of fine sand. It also contains a comparatively high amount of lime, but its sesquioxide content is much lower than that of the Mediterranean terra rossa. It is one of the most fertile soils of the Negev but tends towards salinity when watered unreasonably. At present almost the entire loess area is under cultivation and is characterized by a particular type of weed vegetation.

In the southern Negev, south of Revivim, there occurs a variety of fluviatile loess, redeposited in badly drained depressions and marked by a heavy texture and a fairly high amount (0.5 per cent to 1 per cent) of soluble salts.

The southern and western boundaries of Palestine's loess area merge into the coastal sand dunes, so that a transitional strip consisting of the so-called sandy loess soil (No. 13) comes into prominence. Here the loess soil is covered by a layer of sand that absorbs the sparse rainwater efficiently and protects the underlying loess from excessive evaporation. This is the most fertile soil of the Negev, extensively cultivated and marked by a psammophilous weed vegetation of its own.

Hammadas and Other Desert Soils. Hammadas are climatically conditioned desert soils. They occupy vast areas of the Near Eastern, North African and Central Asian deserts, which have an annual precipitation not exceeding 100 mm. Generally the term "hammada" is applied to plains with a surface cover of stones and pebbles. Yet it should be used in a wider sense, so as to include other desert substrata such as rocky and gravelly hills and also desert formations that have no stone cover but are composed of soft powdery chalks and marls. Among the local hammadas Evenari and Orshansky (1948) have distinguished four varieties: the grit, the salt, the sand, and the non-saline hammada. The latter is almost exceptional in the area under review. There is, however, a far greater number of varieties, since the nature of the hammada depends largely on the lithologic make-up of the stratum. A feature common to almost all varieties of hammada occurring here is the extremely low content of moisture and the abundance of chlorides and sulfates (M. Zohary, 1947b).

Hammadas are mostly devoid of vegetation because of drought and salinity. Where permanent vegetation does occur, it consists of xerophytes exhibiting high osmotic values exceeding the suction force of the soil. Only in the wadis and runnels that traverse the

hammada is the additional moisture supplied by run-on water sufficient to leach the salt and decrease the suction force of the soil (Karschon, 1953).

Hammadas are prevalent in the Negev, the Judean Desert, and in Moav, Edom, and the Arava Valley. The following are the most common varieties:

STERILE LOWLAND HAMMADAS (No. 19). This variety is very common in the southern Negev, Arava Valley, and Edom, where it is confined to gently undulating plains. Its surface cover of stones and gravel consists mainly of angular pieces of flint (Fig. 2). The soil beneath is often fine and mealy, loose or compact, and of gray

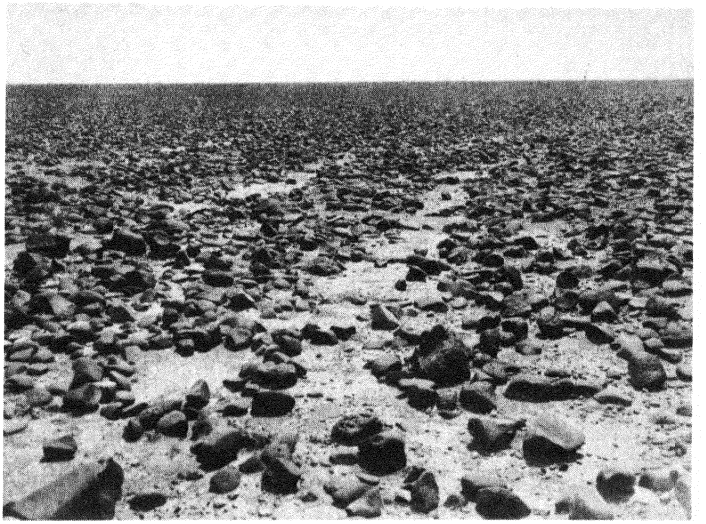


Fig. 2. Barren hammada, north of Ma'an, Edom.

or brown color. It is rich in calcium and contains an amount of soluble salts—mainly sodium chloride—ranging from 0.5 per cent to 4 per cent. Frequently the subsoil is separated from the parent rock material by a crust or concretions of gypsum, occurring at various depths. This type of hammada is altogether plantless, and a relatively rich vegetation is found only in the shallow, salt-free wadis and runnels which traverse it. This vegetation is characterized by sparse *Acacia* trees, *Anabasis*, *Retama* and *Haloxylon* shrubs.

HILLY HAMMADAS (No. 20). This is a variety common in the central and western Negev. Here the vast plateau is cleft deeply into a

series of wadis, ravines, and depressions. The residual portions of the plateau are densely covered with gravel and boulders, overlying a mixture of gravel and silt which contains gypsum. In the valleys a fine-textured aeolic or fluviatile loess is accumulated. Both contain soluble salts ranging from 0.5 per cent to 2 per cent. This type of hammada supports a fairly well-developed vegetation, in spite of its salinity, namely, the ZYGOPHYLLETUM DUMOSI association on the hilltops and hillsides and the HALOXYLETUM ARTICULATI in the adjacent valleys.

HAMMADA-LIKE ROCKY DESERTS (No. 14). The third variety of hammada is less uniform in its physical properties and chemical composition, and is also less clearly defined. It comprises stretches of rocky ground with only small interspaces of soil. This variety occupies large parts of the eastern Negev, the Judean Desert, southern Transjordan, and the Syrian Desert.

HIGHLY GYPSEOUS AND STONELESS SOIL. This soil, which is so common in the eastern part of the Judean Desert and other deserts, can be regarded as another variety of hammada. It is mainly derived from a gypseous rock of the Upper Senonian and supports a specific succulent and gypsophilous vegetation.

Saline Soils (No. 15). The saline soils of Palestine occur on substrata of various origins, such as sands (e.g., Arava Valley), alluvial loams (e.g., Acre Plain), or Lissan marls (e.g., Jordan Valley). They are centered mainly in the lower Jordan Valley but also occupy small areas in the coastal plain. The majority of them are sodium chloride salines, automorphous or hydromorphous according to their genesis.

AUTOMORPHOUS SALINE SOILS. In these the soil salinity is a result of local climatic conditions and petrographic composition of the substratum, unaffected by additional hydropedic processes. The Lissan marls of the higher terraces of the lower Jordan and Arava valleys, for instance, belong to this variety. Their soluble salt fraction reaches a maximum of 2 per cent of dry matter content. Exposed as they are to conditions of extreme drought, they are almost devoid of vegetation—as in the Arava Valley—or elsewhere are only thinly covered by some halophilous shrubs. Broadly speaking, one must also include within this category the aforementioned more or less saline hammadas.

HYDROMORPHOUS SALINES. These can be subdivided into groundwater salines and flooded salines. The former owe their existence to the high table of saline ground water. The salt content of the upper

soil layer rises during the dry season. Ground-water salines are widespread in the lower Jordan Valley (lower terrace), where they may contain as much as 6 per cent of soluble salts. Salines flooded during the whole or part of the rainy season are common in the Dead Sea region and in the Arava Valley, but they also occur in the coastal plain. Their soluble salt content is the highest to be found in Palestine and sometimes reaches 20 per cent. Both varieties have a rich vegetation. The particular plant communities they support will be discussed in Chapter 7.

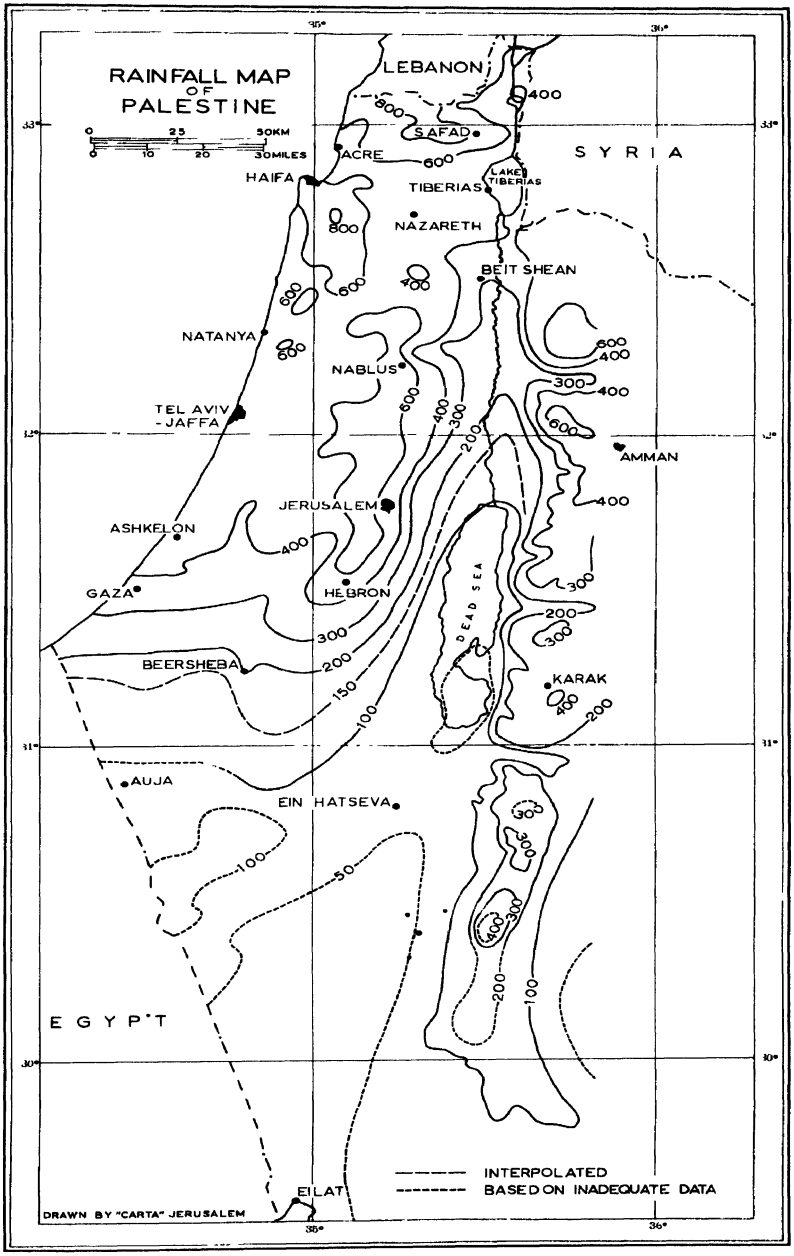
2

Climate and Plant Life

The Nature of Climate

The climate of Palestine as a whole is of the Mediterranean type, marked by a mild, rainy winter and a prolonged dry and hot summer. Geographical latitude, altitude, the blocking effect of mountain ranges, and distance from the Mediterranean Sea are among the factors which modify this climate. The effect of latitude manifests itself in the abrupt north-to-south decrease of the annual amount of rainfall, so that within a range of about four latitudinal degrees rainfall drops from about 1000 mm. to 25 mm. per annum. Temperatures, on the other hand, increase from north to south; the mean annual temperature rises from just below 16° C. in the north to approximately 23° C. in the extreme south of Palestine. In a west-to-east direction, annual rainfall and mean temperatures undergo similar but less regular changes. This is because of the interference of the Israel and Jordan mountain ranges. As a result of their interception of rains, part of the Jordan Valley is turned into a rain-shadow desert. In addition, the mountain ranges limit the tempering influence of the Mediterranean Sea to a narrow strip, leaving the greater part of Palestine open to a wider range of seasonal and diurnal temperatures.

An attempt to divide Palestine into climatic zones according to aridity indices computed by various authors from such data as ratio of precipitation to saturation deficit, etc., has failed for the following reasons: the area is too small and the climatic gradients too steep, and for certain portions of Palestine no accurate data are available. In view of the fact that Palestine's rainfall outbears all other climatic factors in its influence on vegetation, the author follows Blair's (1942) classification with some minor alterations and subdivides Palestine according to the amount of annual rainfall into (1) a subhumid zone with an annual rainfall of 1000–400 mm., (2) a semiarid


RAINFALL MAP
OF
PALESTINE
0 25 30KM
0 10 20 30MILES
LEBANON
SYRIA
SAFAD
ACRE
HAIFA
TIBERIAS
LAKE TIBERIAS
NAZARETH
BEIT SHEAN
NATANYA
NABLUS
TEL AVIV
- JAFFA
AMMAN
JERUSALEM
ASHKELON
GAZA
HEBRON
DEAD SEA
BEERSHEBA
KARAK
AUJA
EIN HATSEVA
EGYPT
EILAT
INTERPOLATED
BASED ON INADEQUATE DATA
DRAWN BY "CARTA" JERUSALEM

Map 3.

zone where annual rainfall is 400–200 mm., and (3) an arid zone with 200–25 mm. of annual rain. These subdivisions happen to coincide more or less with the plantgeographical divisions of Palestine as presented on Map 4.

The annual distribution of rainfall and temperature within each climatic zone is shown in pluviothermic diagrams (Figs. 3–8) representing the respective zones.

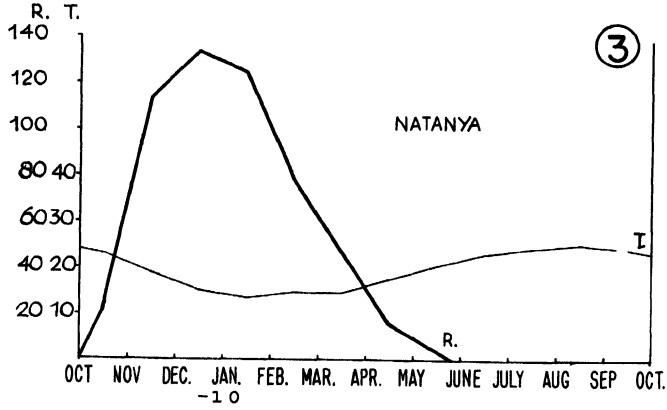
In drawing the diagrams the author has followed Walter (1956a); each point on the ordinate denotes 10 centigrades of temperature and 20 millimeters of rain. The months marked on the abscissa begin with October—the first month of Palestine's rainy season. A glance at the diagrams clearly demonstrates the uniformity of the Mediterranean type of climate with its seasonal division into rainy mild winters and dry hot summers. The variants of this climate are mainly quantitative. The degree of diversion between the rain and temperature lines reflects the degree of humidity in winter and aridity in summer, respectively. Absolute minimum temperatures below zero are also indicated.

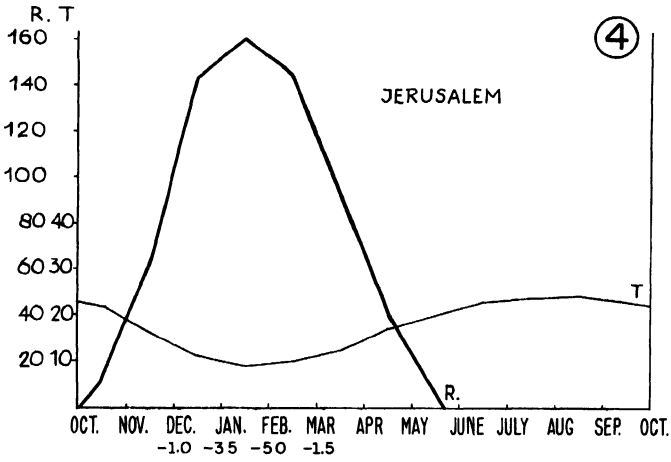
Temperature and Plant Distribution

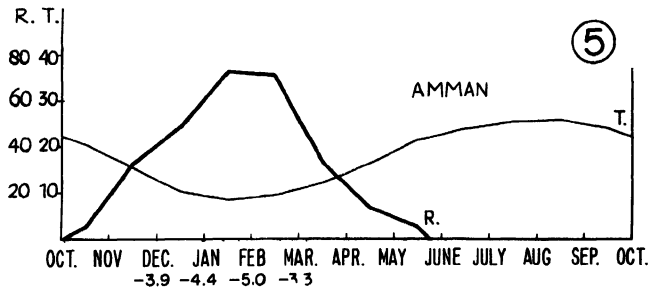
Although plant life is not eliminated anywhere in this country by extremes of temperature, plant distribution is greatly influenced by thermal conditions. For instance, a series of tropical plants, thriving in the southern part of the Jordan Valley, do not advance northward to where winters are colder. Among them are *Maerua crassifolia, Moringa aptera, Acacia raddiana, Balanites aegyptiaca, Salvadora persica, Abutilon muticum, Calotropis procera,* and *Sebestena gharaf.* Very puzzling is the fact that most of these plants are limited to very low altitudes (300-400 m. below sea level), whereas in the central Sahara they reach a considerable height on the mountains (Maire, 1933, 1940). *Balanites aegyptiaca* has been recorded at 1300 m., *Salvadora persica* at 1500 m., *Calotropis procera* at 1800 m., and *Maerua crassifolia* at 1900 m.

Other examples of the part played by minimum temperatures on plant distribution are provided by the QUERCETUM ITHABURENSIS, which is not found at altitudes above 500 m.; ZIZYPHETUM LOTI, which occurs only up to a height of 250 m.; and a whole series of species characteristic of the coastal plain, which do not occur in the mountain belt because of the lower temperatures during the winter.

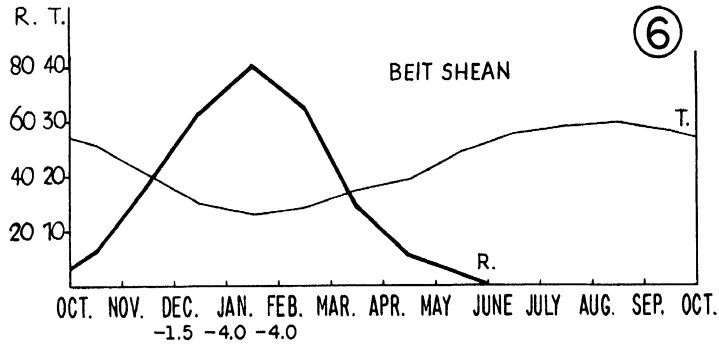
Other typical Mediterranean plants (*Laurus nobilis, Spartium junceum, Pistacia lentiscus,* etc.) are altogether lacking in the Mediterranean territory of Transjordan, probably also because of the minimum winter temperatures. Many tropical swamp plants, among

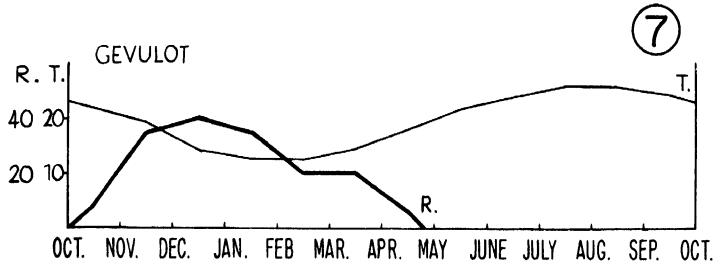


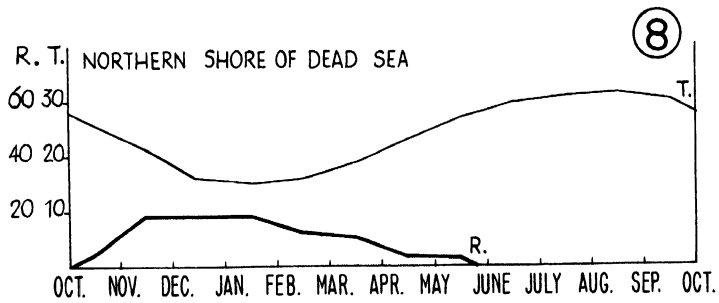




Figs. 3–5. Climadiagrams of the Mediterranean zone. 3, Natanya (coast); 4, Jerusalem (mountains); 5, Amman (continental). R = rainfall in mm.; T = temperature in ° C.







Figs. 6–8. Climadiagrams of the arid and semiarid zones. 6, Beit Shean (Irano-Turanian); 7, Gevulot, approximately 20 km. SE of Rafa (Saharo-Sindian, coast); 8, northern shore of Dead Sea (Saharo-Sindian, interior). R = rainfall in mm.; T = temperature in ° C.

them *Cyperus papyrus,* reach their northern limit of distribution in the swamps of the upper Jordan Valley (Huleh Plain), in spite of the fact that similar edaphic conditions are available further north.

On the other hand, peculiarities in the distribution of certain plants provide examples of the limiting effect of high temperatures. A series of species growing in upper Galilee do not spread southward to Samaria and Judea in spite of the favorable soil and moisture conditions available there. *Juniperus oxycedrus, Paeonia corallina, Sorbus trilobata, Prunus ursina, Gonocytisus pterocladus, Acer syriacum,* and *Asperula libanotica* are examples. Similarly the association of *Quercus calliprinos–Pistacia palaestina* and a number of other plant communities do not occur at altitudes lower than 150 m. above sea level.

Temperature and Phenology

Germination. While some of the phasic phenomena in plant development are conditioned by temperature alone, others, such as germination, depend largely on the combined effect of temperature and moisture.

The majority of local plants germinate in November, as a rule, after the first rains have fallen and temperatures have dropped. However, in years of delayed rains germination may start only in December or even later despite the considerably lower temperatures then prevailing. Moreover, some winter annuals, whose seeds ripen in spring, may germinate soon after ripening, provided sufficient moisture is available. Seedlings of these plants can often be observed among irrigated summer crops. Examples are *Diplotaxis erucoides, Erucaria* spp., *Trifolium* spp., *Malva parviflora, Cephalaria syriaca, Phalaris paradoxa,* and *Lolium temulentum.* Other winter annuals definitely require short exposures to lower temperatures before they can germinate, e.g., *Sinapis arvensis, Hirschfeldia incana,* and *Tetragonolobus palaestinus.* High temperatures—from 20° to 30° C.—are required for germination in a series of summer plants. Examples are: *Atriplex rosea, Amaranthus* spp., *Portulaca oleracea, Heliotropium* spp., *Datura metel, Erigeron* spp., and *Setaria verticillata.*

Bud-Break and Leaf-Fall. Only about half of the arboreal species of the Mediterranean forest and maquis are evergreens. The period through which deciduous trees shed their leaves is largely dependent on end-of-summer temperatures; in most of them leaf-fall occurs between September and December. Duration of dormancy varies with winter temperatures. In mild winters the dormancy period is

cut considerably, and bud-break may sometimes start before the last leaves have been shed, e.g., in *Quercus ithaburensis* and *Amygdalus communis.*

Noteworthy is the large proportion of deciduous species among the Mediterranean "evergreen" wood flora, particularly in view of the fact that their phenological behavior is disharmonious with the local climatic rhythm and confines them to dormancy in the very season—the mild winter—that is most favorable for plant activity. This controversy points to the assumption that these trees, although true and natural components of Mediterranean woods, are alien plants from the historical point of view, e.g., relic species of a Late Tertiary Irano-Turanian invasion. In contrast to the above group, are a number of shrubs and trees which shed their leaves early in summer, e.g., *Lycium* spp., *Anagyris foetida,* and many spartoid shrubs. Facultative leaf-shedders, depending on winter temperatures, are the tropical evergreen *Zizyphus spina-christi* and *Ficus sycomorus.*

Another group of trees are the true evergreens, which usually shed their old leaves in spring or early summer, long after appearance of the new foliage. Examples of these are *Quercus calliprinos, Laurus nobilis,* and *Ceratonia siliqua.*

Almost all dwarf shrubs (chamaephytes) of Palestine vary from the above types and may be classed as heterophyllous evergreens. Their comparatively large winter leaves are shed in early summer and are replaced by smaller, sometimes scalelike, summer leaves crowded together in budlike bodies. Examples of this type, which dominate the vegetation throughout Palestine, are *Poterium spinosum, Thymus capitatus, Thymbra spicata,* and *Cistus* spp. These plants have their main growth period in winter and spring but are also physiologically active in summer, and in this regard their phenological behavior is in full accordance with the climatic rhythm of the area.

Flowering. Most of the plants have their flowering period at the end of the rainy season, between March and May. The influence of temperature on the time of flowering is evident from the fact that the wild and cultivated flora of the coastal plain and the Jordan Valley come into bloom about one month prior to that of the colder mountain range. This is also true of the same species growing under the various conditions of the above zones. Accordingly, field crop and fruit harvests are gathered much earlier in the lowlands than in the mountains with their colder winters. In years with mild winters the flowering season is apt to occur a month or more earlier.

The detrimental effects such untimely blossoming can have on field crops are well known.

The distribution of flowering periods of Palestinian plants is shown in Fig. 9. From this it emerges that: (1) times of flowering are distributed unequally throughout the year, (2) the peak is reached in April, when about 1600 species, including about 1000 annuals, are in flower, (3) flowering is at its lowest in December, and (4) in winter flowering percentages increase with temperature, whereas there is no correlation between flowering and temperature

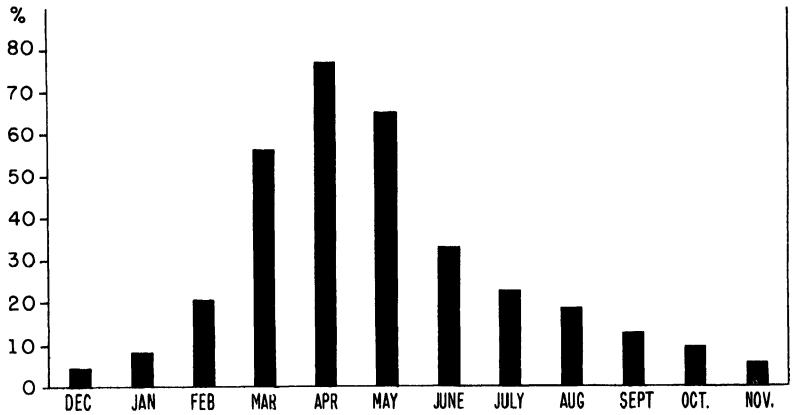


Fig. 9. Monthly distribution of flowering in the flora of Palestine.

during the summer or between flowering and seasonal distribution of rain. The fact that in June, the hottest month of the year, 35 per cent of the flora are still in flower, while in January, one of the rainiest months, less than 10 per cent of the plants are flowering, shows clearly that high temperatures restrict flowering less than do low ones.

According to their flowering period, local plants can be divided into the following groups:

1. The ephemeral group with a flowering season from December to February. This group comprises a considerable number of tiny annuals and geophytes, which complete their life cycle in the early winter months. Whether or not there is a connection between the shortened cycle of those plants and their preference for a shorter photoperiod, is still to be investigated.

2. The spring flowering group, in bloom in March and April, comprises the largest number of species. In addition to annuals and

geophytes, which form its bulk, it includes the majority of the trees and shrubs.

3. The early summer group comprises a series of hemicryptophytes that develop vegetatively during the rainy season but reach their flowering stage only between May and July. In addition to many species of thistles, this group includes xerophytic dwarf shrubs characteristic of the mountains. In this category also belongs the group of summer annuals, most of them weeds.

4. The late summer and autumn flowering group comprises most hydrophytes and some halophytes as well as some psammo- and lithophytes. An interesting group included here are those geophytes that flower before their leaves appear, such as *Biarum, Scilla, Colchicum,* and *Pancratium.*

The factors determining the times of flowering of these groups are probably very complex. In some cases temperature may be decisive and in others temperature and moisture factors may be combined. For a considerable number of plants, however, the time of flowering is not determined by their present-day environment but by endonomic factors, such as the phenological rhythm preserved in the plant from other environments in their past history.

Rainfall and Vegetation

Amount of Rainfall. As has already been mentioned, Palestine's annual amount of rain ranges from about 1000 mm. in the north to 25 mm. in the Gulf of Aqaba. This gradient of decreasing rainfall is much steeper in its northern than in its southern half, yet in the south the decrease is much more decisive on plant life than in the north. In the south, even the smallest deviation from the average makes itself felt in density and development of vegetation, while in the north differences amounting to as much as 200 mm. per annum are hardly reflected in the general appearance of the vegetation. This is self-evident from the fact that depending on soil properties the 100–50 mm. isohyetes constitute the lower rain limit of plant life in Palestine.

Palestine, with the great deserts of Asia and North Africa on its borders, offers the plant geographer an ample opportunity to follow distribution features in the flora and vegetation along rainfall gradients. Hundreds of Mediterranean species are arrested in their southward move by diminishing rainfall. Some of them reach the southern boundary of the Mediterranean territory, while others are detained long before it. The same is true of plant communities, as is illustrated by the following: the *Quercus calliprinos–Pistacia palaestina* maquis association reaches its terminus at the 400–350 mm.

isohyete; the widespread typical Mediterranean dwarf shrub association, POTERIETUM SPINOSI, is detained at the 350–300 mm. isohyete; the ARTEMISIETUM HERBAE-ALBAE at the 200–150 mm. isohyete; and the ZYGOPHYLLETUM DUMOSI at the 100–75 mm. line. Obviously, local topography and nature of soil causes these boundaries to waver slightly on either side of the isohyete.

Among the isohyetes outstanding in their biogeographical importance are the 400–350 mm. isohyete, which is the lower limit of the Mediterranean forest and, at the same time, that of stable dry farming, and the 100–50 mm. isohyete, which constitutes the climatic threshold of plant life in our deserts.

Beyond this limit, however, plant life does not cease entirely but becomes wholly dependent on topography. Wadis and depressions, which collect water draining off from the surrounding area, support a fairly well-developed vegetation. Even depressions hardly perceptible to the naked eye form favorable sites for vegetation. This is also why deserts with rough topography are less bare than those dominated by smooth unbroken plains. Equal importance must be ascribed to physical soil properties in deserts. Moisture-absorbing surface layers, such as sand and fine gravel, are much more favorable to vegetation than exposed, heavy-textured soils.

Another important feature of rainfall affecting plant life is the instability of its total annual amounts. These fluctuations may be so considerable that one year's rain may be no more than a fraction of another year's total (Table 1). This is especially true for the arid and subarid parts of Palestine, as seen from the following figures recorded for the Negev (Ashbel, 1945): Gaza (33 years of measurements)—minimum 238.1 mm., maximum 810 mm.; Rafa (9 years)—minimum 62.9 mm., maximum 367 mm.; Beersheba (28 years)—minimum 129.8 mm., maximum 336.1 mm.; Auja (Nitzana) (13 years)—minimum 10.4 mm., maximum 284.5 mm. In these arid areas a falling short of the average by as little as 20–40 mm. may cripple vegetation and be fatal also to the dry farming scattered in lowlands and depressions. The instability of the annual rainfall in the arid zones makes the desert "blossom" in one year, restricts the annual vegetation to wadis and depressions in others, and almost annihilates plant life in years of extreme drought. Moreover, where a number of dry years follow each other consecutively, certain desert dwarf shrubs desiccate and die off. Thus, the floristic composition of a plant community may alter drastically from year to year.

Seasonal Distribution of Rainfall. The rainy season lasts from October to May, but about 75 per cent of the total amount of rain

TABLE

Rainfall (in mm.) for Selected Localities Representing

Locality		October	November	December	January	February
Atlith (Coastal plain)	Mean	21	94	136	131	79
	Maximum	114 (1942)*	297 (1935)	293	244 (1944)	183 (1934)
	Minimum	0 (1938)	0 (1943)	0 (1934)	55 (1942)	9 (1937)
Hanita (Upper Galilee)	Mean	40 0	125	130	200	130
	Maximum	123 (1942)	343 (1944)	188 (1943)	410 (1947)	393 (1943)
	Minimum	0 (1944)	0 (1943)	4 7 (1943)	94 8 (1941)	40 5 (1947)
Beit Jimal (Judean foothills)	Mean	14.7	72 5	95.0	126	117
	Maximum	129 (1942)	236 (1944)	374 (1941)	276 (1943)	261 (1920)
	Minimum	0	4 9 (1934)	3 4 (1932)	24 5 (1936)	0 (1937)
Jerusalem (Judean Mountains)	Mean	13 0	63.0	144	161	144
	Maximum	84 8 (1942)	193 (1883)	417 (1898)	367 (1897)	320 (1882)
	Minimum	0	0 (1905)	6 0 (1932)	3 0 (1873)	3 8 (1901)
Amman (Transjordan)	Mean	5 5	33.1	49 1	73 1	71.5
	Maximum	54 6 (1942)	137 (1944)	155 (1941)	142 (1944)	191 (1927)
	Minimum	0	0 1 (1934)	0.6 (1932)	13 4 (1936)	5 2 (1940)
Beersheba (Northern Negev)	Mean	5 4	26 0	35 4	54 8	47 2
	Maximum	35 0 (1935)	80.5 (1929)	107 0 (1934)	195 1 (1934)	114 3 (1932)
	Minimum	0	1 0 (1932)	0 (1935)	7 6 (1927)	2.7 (1940)
Beit Shean (Upper Jordan Valley)	Mean	13.0	37.3	63 6	80 2	65 0
	Maximum	75.0 (1932)	131 (1945)	186 (1944)	165 (1943)	175 (1931)
	Minimum	0	0 2 (1943)	9 5 (1932)	15 6 (1946)	9 6 (1947)
Jericho (Lower Jordan Valley)	Mean	3 6	20 4	26 7	37 6	24 6
	Maximum	17 6 (1943)	81 4 (1944)	79 5 (1924)	85 8 (1940)	66 1 (1946)
	Minimum	0	0	0 1	10 8 (1946)	22 (1940)

*Numbers in parentheses denote respective years

falls between December and February. The amounts of rain in particular months vary greatly from year to year. For instance, the January total for Ramle was 300 mm. in one year and 37.2 mm. in another; for Jerusalem readings of 367 mm. and 3.0 mm., respectively, were recorded; the northern shore of the Dead Sea had a January total of 58 mm. in one year and of 4.0 mm. in another. Such fluctuations favor the development of certain plants in particular years. The result is the so-called "flower year," a very striking phenomenon in which certain annual species dominate the landscape at irregular intervals of a few to many years. Annual fluctuations in the rainfall totals of particular months may also bring about prolonged periods of drought within the rainy season. This can be

1

the Main Districts of Palestine (Ashbel, 1951a,b)

March	April	May	June	July	August	September	Annual	Years of Records for Mean Values
26	17	3	–	–	–	–	506	1940–48
104 (1943)	44 (1943)	27 (1938)		–	–	8 (1933)	845 (1944/5)	
0 (1935)	0 (1939)	0	–	–	–	0	263 (1941/2)	
100	35 0	15 0	–	-	–	2 0	777 0	1939–46
140 (1943)	130 (1940)	22 0 (1947)	–	–	–	–	1024 3 (1944/5)	
16 0 (1947)	9 7 (1945)	0	–	-	–	-		
46 0	18 5	2 1	–	–	–	0 1	491 9	1920–48
150 (1939)	53 5 (1935)	12 2 (1945)	-		–	1 5 (1935)	965 3 (1919/20)	
0 (1937)	0	0		–	–	0	232 4 (1946/7)	
93 0	40 0	5.0		–	–	–	663 0	1930–49
314 (1893)	166 (1885)	320 (1887)	-	–	–	28 2 (1932)	1064 (1905)	
3 3 (1925)	0 (1897)	0	–	–	–	-	260 5	
33.0	13 6	4 2	–	–	–	–	283 1	1930–48
96 9 (1902)	54 8 (1937)	30 6 (1946)	–	–	–	-	470 5 (1944/5)	
0 (1927)	0 (1928)	0		–	–	–	118 6 (1940/1)	
21 2	9 8	2 4	–	–	–	–	202 2	1921-48
86 7 (1943)	45 9 (1925)	45 0 (1921)	–	–	–	–	336 1 (1933/4)	
0	0	0		-	-	--	108 7 (1946/7)	
29 7	11 9	4 2	–	–	–	0 4	305 3	1928–48
98 3 (1943)	48 5 (1943)	21 0 (1938)	–		–	3 5 (1932)	528 1 (1944/5)	
0 (1928)	0	0	-		–	–	149 0 (1937/8)	
13 1	7 2	2 5		–	–	–	137.7	1921 48
48.1 (1948)	25 7 (1940)	25.0 (1924)	–	–	–		333 3 (1944)	
0	0	0	–	-	–	–	59 6 (1946/7)	

harmful to vegetation and is also apt to alter the species composition of plant communities from one year to another.

Air Humidity and Dew

There is a gradual decrease in the annual, monthly, and diurnal averages of relative humidity from north to south and from west to east throughout the whole area, excluding the coastal plain. This plain also has a high rate of humidity in the south, which presumably accounts for the high growth rate of many tropical and subtropical plants and certainly also contributes to the comparative fertility of the coastal Negev. The average relative humidity of a summer midday amounts to 65 per cent in Natanya (Sharon Plain) and to 75

per cent in the coastal Negev, while in Jerusalem it is only 35 per cent, and 40 per cent in the Dead Sea Valley (Ashbel, 1951c).

At this point mention must be made of the alleged part played by dew in plant life. According to Ashbel (1951c), there are over 200 dew nights in the coastal plain and much fewer in the interior parts of Palestine. In the years 1943–47, according to Duvdevani (1953), the amount of the yearly dew precipitation, measured by means of the Duvdevani dew gauge, varied from 4.7 mm. in Jericho (lower Jordan Valley) to 29 mm. on Mount Carmel. Average figures of dew measurements during 1945–47 in the Beersheba region and in Gevulot in the Negev amounted to 7 and 15 mm., respectively (Duvdevani, unpublished).

Although according to the above measurements the yearly total of dew is quite negligible, much importance has been ascribed to it by ecologists. Recent measurements of dew absorption by desert plants, however, have led to the conclusion that many plants are unable to absorb dew and that in others the amount absorbed during a dew night is so small that it hardly covers the water loss of one hour's transpiration (Waisel, 1958). It is evident that such amounts do not replenish the summer saturation deficit of plants, with its values of 50–70 per cent.

Climate and Life Forms

Raunkiaer's classification of life forms (Raunkiaer, 1934) has been widely applied for differentiating the physiognomic and ecologic peculiarities of various floras, and for setting up his so-called "biological spectra" used as indicators for phytoclimate. Raunkiaer's normal biological spectrum was computed from the world flora as follows: phanerophytes (Ph) – 46 per cent; chamaephytes (Ch) – 9 per cent; hemicryptophytes (H) – 26 per cent; cryptophytes (C) – 6 per cent; therophytes (Th) – 13 per cent. For comparison, biological spectra of some floras are recorded in Table 2.

Considering the whole question of life forms in regard to ecology and phytoclimate, a number of points became evident:

1. Countries as political entities should not be subject to an analysis of life forms because they are often complex in their plant-geographical make-up. Taking Israel as an example, each of its three plantgeographical territories (see Map 4) yields a different biological spectrum.

2. Percentages of life forms, as represented in Table 2, cannot give a true picture of a phytoclimate, since it is not the numerical proportion of species of an area that counts here but the part played by particular species in the living plant cover. As a matter of fact,

TABLE 2

Biological Spectra for Floras of Various Countries
(Adapted from Raunkiaer, 1934)

Place	Ph	Ch	H	C	Th
Spitsbergen	1	22	**60** *	15	2
Paris Basin	5	3	8	**55**	24
Denmark	7	3	**50**	2	18
Lybian Desert	12	21	20	5	**42**
Palestine	6.6	9.8	24.3	11	**48.3**
Timbuktu	24	**36**	8	6	26
Seychelles Islands	**61**	6	12	5	16

* The bold-type figures indicate the dominating life form (phytoclimatic indicator) in the respective country.

only a very small proportion of the species of the flora builds up the dominant vegetal cover of an area. In Palestine, for instance, the bulk of the plant cover consists of only about 10 per cent of the total number of species. The rest are unimportant or even negligible from the point of view of coverage. Only species of high coverage in plant communities can be used for life-form analysis, and indicate a phytoclimate in the proportions in which they occur.

3. Not all life forms in a given area reflect present climatic conditions in their behavior. In some areas species may also occur in discordance with the particular area's prevailing climatic rhythm because the species are survivors of past geologic climates. Thus the biological spectrum of a flora, so complex in its history, can hardly be used to characterize a present climate.

4. Where floras of arid or subarid regions are concerned, the ecologic value of the various life forms, as understood by Raunkiaer, manifests itself less clearly and loses much of its significance. A classification based on location of renovation buds, their distance from the ground, and the degree of bud protection safeguarded by that distance seems to be of little ecologic importance in arid regions. A distinction between therophytes, hemicryptophytes, and cryptophytes has little ecologic meaning because in all these forms the aerial shoots die off at the end of their vegetative season. Also, the distinction between chamaephytes and phanerophytes with bud location and height of plant as criteria seems to be less significant ecologically than are, for instance, distinctions made between evergreen and deciduous phanerophytes. The ecologic approach to life-form distinction in arid regions has to consider the morpho-ecologic and pheno-ecologic behavior in plants, that is, the changes the plant

body undergoes during the climatic year. Emphasis has to be put not on the protection of buds but on the protection of the whole plant body against drought. Accordingly, the following types, corresponding in part to Raunkiaer's life forms, have been distinguished in the local flora (Orshan, 1953):

a. Leaf-shedding Plants. These coincide more or less with Raunkiaer's phanerophytes, and can be subdivided into evergreen and deciduous plants.

b. Branch-changing Plants. This group includes perennials in which entire branches or parts of them die off with the advent of the dry season. They are replaced by new branches, which develop in the subsequent rainy season. This group corresponds more or less to Raunkiaer's chamaephytes.

c. Shoot-changing Plants. These comprise cryptophytes and hemicryptophytes in which the entire aerial shoot dies off at the end of the rainy or vegetative season.

d. Therophytes (in Raunkiaer's sense). These consist of winter and summer annuals whose entire bodies die off at the end of the growing season.

Each of the above groups of the life forms can be further subdivided into phenological units, according to the season in which parts of the plant body die off. Although these groups have their equivalents in Raunkiaer's classes, it is the reduction the plant body undergoes during the unfavorable season which serves as the basis of classification here.

Considering once more the biological spectrum and its capacity to reflect the phytoclimate of a given region, it must be stated that the above-cited figures clearly point to a therophytic phytoclimate for Palestine. Even if the three main phytogeographical elements of the flora are considered separately, and different biological spectra are arrived at for each territory, all three still indicate a therophytic phytoclimate in Raunkiaer's sense. And this is despite the fact that the Mediterranean territory, as a whole, has a phanerophytic, and the arid regions mainly a chamaephytic, climax vegetation.

This clearly illustrates that by merely grouping the sum total of species of a flora into life forms, without taking into account what proportion of the vegetation they constitute, one can hardly arrive at a true phytoclimatic evaluation of the area. An attempt was therefore made by Orshan (1953) to establish a biological spectrum of the vegetation of the three plantgeographical territories of Palestine by considering only such species that have a high coverage or dominance within their respective communities. His results are shown in Table 3.

TABLE 3

Biological Spectra of Dominants in Various Plant Communities of the Three Plantgeographical Territories in Palestine (Orshan, 1953)

Plantgeographical Territories	Number of Species	Leaf-shedding Plants (%)	Branch-changing Plants (%)	Shoot-changing Plants (%)	Therophytes (%)
Mediterranean	90	16	17	37	30
Irano-Turanian ..	70	4	19	30	47
Saharo-Sindian	71	0	27	13	60

In this way the differences between the spectra of the three territories become very obvious. It is seen that while there is a decrease in the number of phanerophytes, cryptophytes, and hemicryptophytes from the Mediterranean to the Saharo-Sindian territory, there is an increase in the numbers of chamaephytes and therophytes.

3

Flora and Plant Geography

A Short History of Investigation of the Flora

The flora of Palestine has always been a most attractive subject to students and explorers interested both in the natural history of the Near East and in Biblical research. In the following brief account of the most important events in the exploration history of Palestine's flora mention is made only of those works (dealing with the flora of Palestine) which have a scientific approach to the subject.

Among the earliest collectors and explorers the name of Rauwolf (1583) is noteworthy. He journeyed through Palestine, Syria, and Mesopotamia in the years 1573–75. The results of his botanical findings were published by Gronovius in the latter's *Flora Orientalis* (1755).

Strand was the first (1756) to compile a *Flora Palaestina* with the guidance of C. Linné. This was based mainly on the lectures of Linné, the itineraries of Hasselquist, the collections of A. Rydelius and Rauwolf and on the *Hierobotanicon* by Celsius (1745–47). It is a flora which comprises about 600 species, part of them Lebanese plants. Special mention should be made of Hasselquist, a student of Linné, who explored the natural history of a large part of Palestine in the years 1749–52. His valuable book *Iter Palaestinum* was first published in 1757, with the editorship of Linné. Another eminent botanist, also a student of Linné, was Forskål, who explored Egypt and Arabia. His *Flora Aegyptiaco-Arabica,* published after his death by C. Niebuhr in 1775, and his collections remain a first-hand source of information up to the present day also for the flora of Palestine.

During the first half of the nineteenth century Palestine's flora became the focus of attention of many eager explorers, botanists, and collectors. Aucher-Éloy in 1830 (1843), Kotschy in the years 1836, 1842, and 1855 (1861), J. R. Roth in 1837, and others passed

through parts of the Levant, including Palestine. Their collections, have served as a basis for the conclusive work of the eminent Swiss botanist, Boissier—the *Flora Orientalis,* published during the years 1867–88.

The activities of Boissier, who made extensive investigations in this region in 1846, mark a special period in the history of the botanical exploration of Palestine. The great merit of Boissier lies in his monumental *Flora Orientalis,* in which all previous botanical findings of the region have been incorporated and critically revised. Up to the present day this book remains the only comprehensive and reliable standard work for all students of the Middle Eastern flora.

During and after the publication of the *Flora Orientalis,* floristic investigation of Palestine has continued. A series of great travelers and botanists explored Palestine adding new floristic or geographical data. Canon Tristram visited several parts of Palestine in 1863–64 and 1872 and published his accounts in his *The Fauna and Flora of Palestine* (1884). This work, so highly appreciated by local zoologists, unfortunately includes many incorrect botanical data. On the other hand, the floristic accounts of Barbey and Barbey (1882) and the work of Hart on the fauna and flora of Sinai, Petra, and the Arava Valley (1891) are most important contributions to the flora of Palestine, at that time still inadequately known.

During the two last decades of the nineteenth century a series of botanical investigations in Cyprus, southern Turkey, Syria, Palestine, and Sinai were carried out by Post, lecturer at the American College in Beirut (Lebanon), who set up a valuable herbarium in the college. The results of his investigations were published in the *Plantae Postianae* (1890–1900, partly in collaboration with Autran), and also in the *Flora of Syria, Palestine and Sinai* (1896). This latter work was the first complete flora for a specific area within the region covered by the *Flora Orientalis.* Including in addition to his original discoveries the data recorded by Boissier and other sources, Post's *Flora* is still used as a manual and reference book today.

Since the beginning of the twentieth century floristic research has adopted more critical methods and a more modern taxonomical approach. Valuable contributions to the local flora have been supplied by Bornmueller (1898, 1912, 1913, 1914, 1921, etc.), known as one of the authorities on the Middle Eastern flora.

Aaronsohn, a botanist and agronomist resident in Palestine, carried out his investigations mainly during the years 1905–15. He traveled extensively in and outside Palestine and set up a herbarium at Zikhron Ya'aqov, near Haifa. The results of his research on Palestine's flora were published mainly after his untimely death by Oppen-

heimer (1930) and by Oppenheimer and Evenari (1940), who edited his work and introduced numerous additions of their own. In these writings many new geographical data for Palestinian plants are recorded and some new species described.

In the years 1909–10 Nabelek made his botanical explorations in the Near Eastern countries and as a result published his *Iter turcico-persicum* (1923, 1925, 1926, 1929). This comprises several data bearing in particular on southern Transjordan, which had been little explored up to that time.

Additions to the flora of Palestine have also been made by Dinsmore, who was the first to compile a catalogue of the Palestine flora (1912). One of Dinsmore's most important contributions is his second revised edition of Post's *Flora of Syria, Palestine and Sinai* (1932–33), which comprises numerous new references and a revised nomenclature. Specimens of his collection are found in many of the great herbaria. Recent advances in floristic research have been made by Samuelsson (1935, 1943) as well as by Rechinger fil. (1949).

With the establishment of the Department of Botany, first attached to the Institute of Agriculture and Natural History in Tel-Aviv, and later transferred to the Hebrew University in Jerusalem, a rapid advance in floristic research was made. During the years 1926–60 the staff of this Department explored the flora and vegetation of most parts of Palestine and the neighboring countries with the aim of setting up a herbarium of Palestine and of Middle Eastern countries. As a result many species were recorded for the first time in the area, and some new species and genera described by Eig (1938c, 1938d, 1948), Eig and Feinbrun (1940), Eig and Zohary (1939), Feinbrun (1944, 1944–45, 1947, 1949), D. Zohary and De Angelis (1952), M. Zohary (1932, 1941), and M. Zohary and Davis (1947). With a relatively comprehensive herbarium at hand, some monographical studies on complex or little understood genera could be carried out. Revisions have been published by Eig on *Aegilops* (1929), *Erodium* (1932), *Anthemis* (1938a), *Picris* (1938b), *Onopordon* (1942), *Scrophularia* (1944), Chenopodiaceae (1945), *Astragalus* (1955); by Feinbrun on *Bellevalia* (1938–40), *Poa* (1940), *Ornithogalum* (1941), *Allium* (1943, 1948), *Rhamnus* (1945), *Colchicum* (1953, 1958), *Crocus* (1957); by M. Zohary on *Plantago* (1938), *Pistacia* (1952b), *Tamarix* (1956), *Retama* (1959). The study of native species has been summarized in *The Plants of Palestine: An Analytical Key* and its second edition, *Analytical Flora of Palestine*, and *A New Catalogue of Palestine Plants* (Eig, Zohary, and Feinbrun, 1931, 1948a, 1948b).

The Flora in Figures

The flora of Palestine comprises 718 genera and about 2250 species of vascular plants. These figures are rather high when compared with those for countries twice or more times the size of Palestine. According to Good (1947), the number of species of the British Isles is about 1750, Denmark 1600, Germany 2680, and Poland 2000. For Syria, including Lebanon, 2865 species have been recorded, for Iraq about 1800, and for Egypt about 1500. Taking into account that more than half the area of Palestine is desert with only a meager flora, the relative concentration of species is amazing. The fact that more than 1000 species of vascular plants, dispersed over 70 families, have been found within an 8 km. radius of Jerusalem, illustrates this point.

Reasons for this density in species are to be sought in the unique position of Palestine, which constitutes a meeting area of three plantgeographical regions: the Mediterranean, the Irano-Turanian, and the Saharo-Sindian. As shown below, not only are the floras of each of the three regions richly represented, but a large number of bi- and pluriregional species also occur here. The topographical diversity of Palestine, which creates varied ecologic conditions within limited areas, also contributes to the abundance in species. The botanist traveling through this area is struck by the suddenness with which the various floras replace each other. On a 100 km. stretch of the highway from the Mediterranean coast to the shores of the Dead Sea he first encounters a typical sand dune vegetation, consisting of Mediterranean and Saharo-Sindian species. Further east he passes a broad belt of alluvial soils, with its rich weed flora and an abundance of pluriregional types. Ascending the Judean Mountains, he comes across the Mediterranean forest and maquis vegetation in various stages of successional development. Descending from the mountains toward the Judean Desert, he suddenly finds himself in an Irano-Turanian flora and vegetation and then enters a characteristic Saharo-Sindian desert landscape with hammadas, salines, and green patches of tropical savannah.

Furthermore, there is the factor of paleo-plantgeography. The flora of Palestine has undergone many changes in its composition since the Early Tertiary. Each period has had its invasions and retreats, and each change has left its relics. An analysis of the Palestine flora into its historical elements, to be discussed in Chapter 3 has revealed the presence of a series of groups that have their origin in different ancient floras and have their advent in Palestine in various geologic periods.

Agriculture, in the course of its long history, has also contributed to an enrichment in species. Numerous instances of this can be observed in segetal and ruderal habitats. While some of these species were introduced unintentionally from remote parts, others have penetrated into Palestine from adjacent regions after the local vegetation had been devastated by man.

There are 114 families in the flora, which is a proportionally high figure for Palestine's 2250 species. The Balkan Peninsula's 6530 species, for instance, belong to only 126 families (Turrill, 1929). That means that the average number of species per family is 18.1 in Palestine and 51.8 in the Balkans. The number of genera is also high in comparison with that of the species. Thonner (ex Good, 1947) gives an average of 13.6 species per genus for the total plant world, while for the local flora the average is only 3.13. The generic coefficient, as understood by Jaccard (1940), i.e., the number of genera per each 100 species, is 31.9 for the Palestine flora but only 14.6 for that of the Balkan Peninsula. In the desert parts of Palestine the generic coefficient is higher still; for instance, in the lower Jordan Valley it is 66 per cent.

The most dominant families are the Compositae with 96 genera and 260 species; Gramineae, 87 genera—198 species; Leguminosae, 62 genera—268 species; Umbelliferae, 52 genera—98 species; Cruciferae, 63 genera—124 species; Labiatae, 23 genera—99 species; Caryophyllaceae, 29 genera—97 species; Liliaceae, 23 genera—97 species; and Boraginaceae, 23 genera—59 species. There are 45 families represented by one genus only. Richest in species are the following genera: *Astragalus* 44, *Trifolium* 40, *Silene* 36, *Euphorbia* 31, *Allium* 25, *Galium* 24, *Centaurea* 24, *Medicago* 23, *Salvia* 22, *Convolvulus* 21, *Anthemis* 20, *Vicia* 20, *Trigonella* 19, *Erodium* 19, *Ranunculus, Cyperus, Plantago*—18, *Ononis* 16, *Bromus* 15, *Iris* 13, *Heliotropium* 12, *Reseda* 12, *Orchis* 11, *Verbascum* 11, *Aristida* 10, and *Bellevalia* 10.

The Plantgeographical Elements of the Flora

The plantgeographical diversity of the Palestine flora was already recognized by the earlier explorers, e.g., Boissier (1867), Grisebach (1884–86), and others. Tristram (1884) was among the first to devote special attention to this subject. Post (1889) also published an account of the phytogeography of Syria, Palestine, and Sinai, and roughly outlined the various constituents of the region's flora. The first to give a fairly detailed analysis of the flora of Sinai and southern Palestine was Hart (1891). But the most comprehensive and modern analysis of the flora was made by Eig (1931–32), who de-

fined its plantgeographical groups and subdivided the country into three plantgeographical territories. Along the lines of Eig (1931–32), some of the most outstanding plantgeographical features of the flora are pointed out in the following discussion. The regions concerned with the plant geography of the Palestine flora are the Eurosibero-Boreoamerican, the Mediterranean, the Irano-Turanian, the Saharo-Sindian, and the Sudanian.

The Eurosibero-Boreoamerican Region. This occupies the greatest part of the Northern Hemisphere, stretching from the Pacific coast of Siberia to that of North America. Its flora and vegetation have been described by various authors. From a floristic point of view there is every justification for designating the Eurosiberian part as an independent region. This separation has been proposed by Engler and Diels (1936), Alechin (1950), and others.

The Mediterranean Region. This region is taken here in its narrower limits as conceived by Boissier (1867), Grisebach (1884–86), Braun-Blanquet (1923, 1951a), Eig (1931–32), and others, and not as by Engler and many Russian phytogeographers who also include within this region some parts of anterior Asia (Iraq, Iran, etc.). It is a region well defined ecologically, notably by its clearly biseasonal climate and by the occurrence of the terra rossa soil type. It comprises a rich flora and abounds in endemic genera and species. Evergreen sclerophyllous forest and maquis climaxes are most characteristic of this region. Although uniform in its gross ecologic features, its division into eastern and western subregions has a sound floristic as well as historical basis (Markgraf, 1934). The boundaries of these subregions run from the west of the Balkan Peninsula to the east of Tripolitania (Eig, 1931–32). Subdivision into a northern and a southern subregion is less well founded.

The Saharo-Sindian Region. (Eig, 1931–32.) This coincides with the "Wüstengebiet" of Grisebach and approximates the "Nord Afrikanisch-Indisches Vegetationsreich" of Engler and Diels (1936). It extends from the Atlantic coast of North Africa, through the Sahara, the Sinai Peninsula, extratropical Arabia, southern Iraq, Iran, and Baluchistan to Sind. Ecologically and floristically, this region is fairly well defined but its boundaries are not clear everywhere. It is comparatively poor in endemics. Although a notable part of its flora extends throughout the entire region, its division into western, middle, and eastern subregions, which was attempted by Eig and later adopted by a number of North African botanists, seems to be justified floristically.

The Irano-Turanian Region. (Eig, 1931–32.) This region concurs roughly with the "Steppengebiet" of Grisebach (1884–86), who included the entire strip of steppes and deserts that extends from the countries at the lowermost part of the Danube in the west to the tributaries of the Amur in the east. Boissier (1867), who considered this region a natural unit and referred to it as *"région orientale proprement dite,"* also suggested that it has a close correlation with the interior plateau of Algeria. This plateau of "Mauritanian Steppes," included by Eig (1931–32) within the Saharo-Sindian region, is now considered part of the Irano-Turanian region by the author (M. Zohary, 1950a) and by others. In contrast to the Saharo-Sindian, the Irano-Turanian region is the center of origin of numerous genera and species. To mention only three: *Astragalus* is represented by about 1000 endemic species, *Centaurea* by 200, and *Cousinia* by 160 to 180. A large number of endemics are also found in the genera *Chesneya, Oxytropis, Acantholimon, Calligonum, Atraphaxis,* and many others. Vegetation consists here mainly of herbs and dwarf shrubs, while wood climaxes are exceptional. The region is of such striking floristic diversity that it has been found necessary to divide it further into a series of subordinate units, but there is a divergence of opinion as to the delimitation and number of these units. Relying upon the data of Boissier (1867), Grisebach (1884–86), Grossheim (1936), Popov (1927), and Gajewsky (1937), as well as on our own findings, a distinction of the following subregions seems feasible: Mauritanian Steppes; Mesopotamian, Irano-Anatolian; Turanian (Aralo-Caspian sensu stricto); Central Asian; and Mongolian.

The Sudanian Region. This was classed by Eig (1931–32), together with the Deccan Plateau of India, as the Sudano-Deccanian region. In a recent paper (Gruenberg-Fertig, 1954) its Sudanian part, comprising the West Sudanian and the Eritreo-Arabian subregions, is considered to be a separate region. This occupies part of tropical Africa, north of the equatorial rain forest region, as well as the southwestern corner of Arabia, southern Iran and Baluchistan. The tropical flora of Palestine belongs partly to the Omni-Sudanian and the Eritreo-Arabian elements, and partly to bi- and pluriregional tropical groups.

The Plantgeographical Groups

A plantgeographical analysis of the Palestine flora reveals the existence of uni-, bi-, and pluriregional groups. The following are the numerical proportions of these groups:

1. The uniregional groups	
Mediterranean element	863 species
Saharo-Sindian element	299
Irano-Turanian element	309
Eurosiberian element	15
Sudanian element	20
Total	1506 species
2. Bi- and pluriregional groups	
a. Subtropical groups:	
Mediterrano–Irano-Turanian	367 species
Mediterrano–Saharo-Sindian	9
Irano-Turano–Saharo-Sindian	35
Mediterrano–Irano-Turano–Saharo-Sindian	4
Total	415 species
b Subtropical-Boreal groups	
Mediterrano-Eurosiberian	15 species
Mediterrano-Irano-Turano-Eurosiberian	97
Total	112 species
c. Subtropical-Tropical * groups	
Saharo-Sindo–Sudanian	21 species
Saharo-Sindo–Tropical	1
Mediterrano–Tropical	10
Mediterrano–Irano-Turano–Tropical	24
Mediterrano Saharo-Sindo–Tropical	2
Mediterrano–Irano-Turano–Saharo-Sindo–Tropical	10
Saharo-Sindo–Irano-Turano–Tropical	1
	69 species
d. Borealo-Tropical groups	85 species
e Tropical groups (bi- and pluriregionals)	53 species
Miscellaneous	9 species

* Groups of plants occurring in several tropical regions of Africa or of Africa and Asia are here referred to as tropical.

Of the above-enumerated groups, only three, namely, the Mediterranean, the Irano-Turanian, and the Saharo-Sindian, are confined to particular territories in Palestine. The others are scattered throughout Palestine or occupy special habitats within those territories. In the following, some plantgeographical data are recorded for the above groups.

The Mediterranean Element. Among the Mediterranean element of Palestine the following six groups have been distinguished by Eig (1931–32): Sub-Mediterranean, Omni-Mediterranean, West Mediterranean, East Mediterranean, North Mediterranean, and South Mediterranean.

THE SUB-MEDITERRANEAN GROUP. About 160 Mediterranean species also penetrate into some countries adjacent to the Mediter-

ranean region. Particularly interesting are the Mediterranean littoral species which recur in the Atlantic sector of the Eurosiberian region, e.g., *Glaucium flavum, Cakile maritima, Euphorbia peplis, E. paralias, Eryngium maritimum, Crithmum maritimum, Statice limonium, Centaurium maritimum, Inula crithmoides, Diotis maritima, Juncus subulatus,* and *Pancratium maritimum.* Other examples are segetals such as *Thesium humile, Adonis autumnalis, Raphanus raphanistrum, Fumaria capreolata,* and *Ridolphia segetum.* Noteworthy among the Sub-Mediterranean species, recurring in some Irano-Turanian countries, are segetals and components of primary vegetation preserved in Mediterranean enclaves of the Irano-Turanian region, e.g., *Pinus brutia, Juniperus oxycedrus, Psoralea bituminosa, Putoria calabrica, Stipa aristella,* and *Oryzopsis coerulescens.*

THE OMNI-MEDITERRANEAN. This group, which also comprises about 160 species, is widespread over the Mediterranean region. Many of them are leading plants in local plant communities, e.g., *Pinus halepensis, Juniperus phoenicea, Calycotome villosa, Ceratonia siliqua, Pistacia lentiscus, Rhamnus alaternus, Cistus villosus, Lavandula stoechas, Thymus capitatus,* and *Viburnum tinus.* Many species of this group are confined to the coastal plain. Examples of these are *Matthiola tricuspidata, Ononis variegata, Orlaya maritima, Statice sinuata, S. virgata, Alkanna tinctoria, Ajuga iva, Crucianella maritima, Scleropoa maritima, Avena longiglumis, Sporobolus arenarius, Cyperus mucronatus, Leopoldia maritima,* and *Narcissus serotinus.* There are no deciduous trees among the Omni-Mediterranean group.

THE EAST MEDITERRANEAN (INCLUDING THE SUB-EAST MEDITERRANEAN). This group is the most prevalent element in the Palestine flora, and includes the majority of Palestine's endemic species. It comprises 485 species, many of them important components of the vegetation. Examples are the following leading species of the maquis: *Quercus calliprinos, Q. boissieri,** *Q. ithaburensis, Platanus orientalis, Prunus ursina, Cercis siliquastrum, Pistacia palaestina, Rhamnus palaestina, Acer syriacum, Arbutus andrachne,* and *Styrax officinalis,* as well as the dominant species of the garigue and batha formations: *Poterium spinosum, Euphorbia thamnoides, Hippomarathrum boissieri, Anchusa strigosa, Alkanna strigosa, Salvia triloba, Phlomis viscosa, Thymbra spicata, Teucrium creticum, Majorana syriaca,* etc. Also belonging to this group are dominant species of the litho- and chasmophytic plant communities: *Arenaria graveolens, Dianthus pendulus, Micromeria serpyllifolia, Ballota rugosa,*

* For systematic treatment of this species, see Zohary (1961).

Hyoscyamus aureus, Michauxia campanuloides, Varthemia iphionoides, Centaurea speciosa, and others.

Many of the local weeds belong to the East Mediterranean group, e.g., *Silene crassipes, Medicago galilaea, Euphorbia cybirensis, Eryngium creticum, Tordylium aegyptiacum, Exoacantha heterophylla, Cachrys goniocarpa, Astoma seselifolium, Convolvulus hirsutus, Heliotropium villosum, H. bovei, Molucella laevis, Carthamus tenuis, Centaurea verutum,* and *Cynara syriaca.*

A characteristic feature of this group is the high number of geophytes (over 12 per cent). Among them *Lilium candidum, Hyacinthus orientalis,* eight species of *Iris,* four of *Colchicum,* and four of *Crocus* are worthy of mention.

THE WEST MEDITERRANEAN. According to Eig (1931–32), this group comprises only 14 species and plays almost no part in the vegetation cover of the country. One may consider some of them, such as *Ophioglossum lusitanicum* and *Euphorbia dendroides,* as being relics of a more humid period, during which local climatic conditions were more favorable for mesic species than they are today.

The North Mediterranean group, comprising 30 species, and the South Mediterranean group, with 14 species, are vegetationally unimportant.

The Saharo-Sindian Element. In Palestine, the Saharo-Sindian element comprises only 299 species, i.e., 13 per cent of the total flora, despite the fact that the Saharo-Sindian territory of Palestine occupies more than half the surface area of the country. Eig (1931–32) has distinguished four groups among this element: the Omni-Saharo-Sindian, and the West, East, and Middle-Saharo-Sindian. He refers the bulk of the Palestine Saharo-Sindian element to the latter. Although the tripartition of the Saharo-Sindian region is still to be reexamined with regard to its lines of demarcation, it is obvious that there are three distinct floristic centers within this region.

As has already been pointed out by Eig (1931–32), Maire (1933, 1940), and others, the Saharo-Sindian flora is less autonomous in its origin than are those of the neighboring regions, and many of its species and genera are derived from the Mediterranean, Sudanian, and partly also from the Irano-Turanian stock. Examples of the Mediterranean derivatives are species of the genera: *Paronychia, Silene, Matthiola, Medicago, Lotus, Ononis, Erodium, Daucus, Origanum, Thymus, Anthemis, Picris,* etc.

Capparis, Cleome, Gomphocarpus, Caralluma, Trichodesma, Iphiona, Varthemia, and *Tetrapogon,* are examples of genera of Sudanian or otherwise tropical origin.

Among Irano-Turanian derivatives mention may be made of species of the genera *Calligonum, Suaeda, Salsola, Haloxylon, Anabasis, Astragalus, Tamarix, Heliotropium, Onopordon, Echinops,* and *Carthamus.*

There is also some affinity to the South African flora as suggested by the occurrence of the genera *Aizoon, Mesembryanthemum, Notoceras, Caylusea, Neurada, Citrullus, Ifloga, Aristida,* and others. However, there are a fair number of genera autochthonous in the Saharo-Sindian region, e.g., *Gymnarrhena, Pteranthus, Gymnocarpos, Sclerocephalus, Anastatica, Zilla, Savignya,* and others.

While Sudanian derivatives seem to have been formed all along the Saharo-Sudanian border, the Saharo-Mediterranean line of contact is limited mainly to two sectors, namely, northwestern Africa and the south of Palestine. It is in these sectors that Mediterranean derivatives within the Saharo-Sindian flora are accumulated. Irano-Turanian derivatives in this flora have been supplied mainly from the Mesopotamian and Turanian stocks.

The most important species in the Saharo-Sindian flora of Palestine are *Calligonum comosum, Anabasis articulata, Suaeda asphaltica, S. vermiculata, Salsola tetrandra, S. rosmarinus, Haloxylon persicum, H. salicornicum, Chenolea arabica, Traganum nudatum, Halogeton alopecuroides, Gymnocarpos fruticosum, Zilla spinosa, Retama raetam, Fagonia mollis, Zygophyllum dumosum, Nitraria retusa, Convolvulus lanatus, Danthonia forskahlei, Aristida scoparia,* and many others. The low percentage of geophytes, amounting to about 4 per cent among the Saharo-Sindian flora, is remarkable.

The Irano-Turanian Element. The country's Irano-Turanian element, including the Sub-Irano-Turanian group, comprises 309 species, i.e., over 13 per cent of the total flora of the country. When the 406 bi- or triregional species of the Mediterrano–Irano-Turanian, Irano-Turano–Saharo-Sindian, and the Mediterrano–Irano-Turano–Saharo-Sindian groups are added to that number, the affinity of the local flora to that of the Irano-Turanian region becomes strikingly apparent. In contrast to the Mediterranean and Saharo-Sindian species, the Irano-Turanian ones are rather restricted in their range of distribution, and there are scarcely any instances of Omni-Irano-Turanian expansion. The bulk of this element in Palestine belongs to the Mesopotamian, the Irano-Anatolian, and the Mauritanian Steppes groups.

THE MAURITANIAN STEPPES SUBREGION. This occupies a belt of considerable width in North Africa, notably in its western part. The flora of this subregion is also marked by a series of generic and spe-

cific endemics. In Palestine the Mauritanian Steppes element is represented by about 30 species, many of them dominants in the local vegetation. Examples are *Ephedra alte, Noëa mucronata, Haloxylon articulatum, Salsola vermiculata, Pistacia atlantica, Rhus tripartita, Zizyphus lotus, Salvia lanigera, Marrubium alysson, Linaria aegyptiaca, Artemisia herba-alba,* and *Achillea santolina.* There is also a striking resemblance between the vegetation of the local Irano-Turanian territory and that of certain parts of the Mauritanian Steppes.

THE MESOPOTAMIAN SUBREGION. This comprises the Irano-Turanian territory of the Syrian Desert, the whole Jezireh (upper Mesopotamia), and parts of the plains in southern Anatolia and southwestern Iran. This subregion has a considerable number of endemics and some particular plant communities by which it is fairly well distinguished from the above-mentioned subregion. In comparison with the Irano-Anatolian and even the Turanian subregions, it is poor in species.

There are 100 or more species which represent the Mesopotamian element in Palestine, and the majority of the Irano-Turanian endemics in Palestine show Mesopotamian affinities. The flora of this subregion includes a remarkable proportion of herbaceous segetals which have also penetrated into the Mediterranean territory. Others of its species are associates of various herbaceous steppe communities, but there are scarcely any leading species among them. There are, however, a considerable number of species common to both above subregions, so that their separation into two subregions is still tentative.

THE IRANO-ANATOLIAN SUBREGION. This comprises mainly the mountainous area of interior Anatolia, Armenia, and the Iranian Plateau (exclusive of certain parts of eastern Iran and western Afghanistan). Parts of southern Transcaucasia may also be included within the Irano-Anatolian subregion. Its outlines coincide with those defined by Boissier (1867) as "Sous-région de Plateaux" as well as with those referred to by Hayek (1926) and Rikli (1913) as "Armenisch-Persisches Hochland." Gajewsky (1937), on the other hand, separates the area into Iranian and Armeno-Anatolian subregions.

Characteristics of the subregion are its high mountain ranges alternating with plains and plateaus of varying altitudes and badly drained valleys and basins. It harbors the most manifold flora of the Irano-Turanian region and is one of its largest centers of speciation in the region. Many endemic species belonging to the genera *Astrag-*

alus, Acanthophyllum, Onobrychis, Hedysarum, Acantholimon, Cousinia, Centaurea, Jurinea, Helichrysum, and many others are centered here.

In Palestine this subregion is poorly represented, owing to the rarity of high mountains. An outpost of this element, which is nearest to Palestine, is Mount Hermon. Among the Irano-Anatolian species found in Palestine are *Atraphaxis spinosa, Pterocephalus pulverulentus, Buffonia virgata, Delphinium antheroideum, Erysimum crassipes, Astragalus bethleemiticus, A. deinacanthus, Euphorbia macroclada, Daphne linearifolia, Scutellaria fruticosa, Thymus syriacus, Phlomis orientalis, Pyrethrum santolinoides,* and *Cousinia hermonis.* Most of them are confined to the higher altitudes of Transjordan and the Negev.

The remaining subregions of the Irano-Turanian region are also poorly represented in Palestine. Only the Turanian subregion (Aralo-Caspian sensu stricto) shows some floristic affinity to Palestine, but rather to its Saharo-Sindian than to its Irano-Turanian flora. Thus a series of genera, which have their highest concentration of species in the Turanian subregion, are characteristic of halophytic and psammophytic habitats in the Saharo-Sindian territory of Palestine, e.g., *Calligonum, Haloxylon, Suaeda, Salsola, Anabasis, Nitraria, Zygophyllum, Tamarix,* and others. These facts lend some support to the view expressed by Grossheim (1936) that the Turanian subregion is to be attached to the Saharo-Sindian region.

The Eurosiberian Element. This element is represented in Palestine by 15 species. Most of them are hydrophytes of little vegetational importance. A more prominent part in the hydrophytic vegetation is played by the many Borealo-Tropical and Borealo-Subtropical pluriregional plants which suggest a Eurosiberian origin.

The Sudanian Element. This is represented in Palestine by 20 species, many of them trees and shrubs, such as *Maerua crassifolia, Moringa aptera, Acacia tortilis, Balanites aegyptiaca,* and *Zizyphus spina-christi.* Most of them are conspicuous in the tropical oases of the Jordan Valley. Since these oases constitute the northernmost outpost of the Sudanian flora, some data as to the northernmost limits reached by some of these plants in Palestine may be of interest:

Zizyphus spina-christi	33° 20′	*Indigofera argentea*	31° 36′
Acacia albida	32° 30′	*Tephrosia apollinea*	31° 36′
Balanites aegyptiaca	32° 28′	*Maerua crassifolia*	31° 28′
Acacia tortilis	31° 51′	*Acacia laeta*	31° 3′
Loranthus acaciae	31° 51′	*Capparis cartilaginea*	30° 40′
Moringa aptera	31° 50′		

The Bi- and Pluriregional Groups of Palestine. The previously discussed groups are uniregional, i.e., each group is more or less

confined to a single plantgeographical region. The sum total of uniregional species enumerated so far amounts to 1506, which is 67 per cent of the flora. The remaining 33 per cent of species of the local flora have a wider range of distribution and extend over two or more plantgeographical regions. The presence of bi- and pluriregional groups in Palestine is not necessarily the result of its particular phytogeographical position. Each plantgeographical region harbors, in addition to the uniregional species which constitute its floristic element, a considerable number of bi- and pluriregionals, or interregionals, as they may generally be termed.

Most interregionals in the Palestine flora are hydrophytes, segetals, ruderals, lithophytes, as well as plants occurring in earlier stages of seral communities and members of open plant communities in general. The wider range of climatic conditions under which these plants can thrive seems to be counterbalanced by their dependence on specific edaphic conditions. The lack of competition met with in such habitats can be another reason for their wide range of distribution. About 150 of Palestine's pluriregional species are hydro- and halophytes. They belong mainly to the Borealo-Tropical, the Borealo-Subtropical and Tropical groups. Many of them are rather prominent in Palestine's vegetation. While most of the tropical pluriregional hydrophytes (e.g., *Polygonum acuminatum, P. lanigerum, P. senegalense, Nymphaea caerulea, Cyperus papyrus, C. alopecuroides, C. latifolius,* and *C. lanceus*) reach their northern limit of distribution here, the Borealo-Tropical group with *Equisetum ramosissimum, Phragmites communis, Panicum repens, Scirpus maritimus, S. lacustris, Schoenus nigricans, Cladium mariscus, Eleocharis palustris,* many species of *Potamogeton, Lemna,* and others) extends much further south.

There are roughly 200 segetal and ruderal species among the bi- and pluriregionals. The Borealo-Tropical group comprises many of them, e.g., *Chenopodium album, C. murale, Urtica urens, Polygonum aviculare, Amaranthus retroflexus, Portulaca oleracea, Stellaria media, Capsella bursa-pastoris, Anagallis caerulea, Convolvulus arvensis, Cynodon dactylon,* and others. Many more segetals and ruderals are included in the Borealo-Subtropical group, of which the following may be mentioned: *Sisymbrium officinale, Lepidium latifolium, Geranium dissectum, G. molle, Erodium cicutarium, Euphorbia helioscopia, E. peplus, Malva silvestris, M. neglecta, Conium maculatum, Galium aparine, Senecio vulgaris, Eragrostis minor, Lolium temulentum,* and *Hordeum murinum.*

Among the biregionals, especially among the Mediterrano–Irano-Turanian group, are found the largest numbers of segetals and ruderals. Examples are *Polygonum equisetiforme, Silene conoidea,*

S. longipetala, Glaucium corniculatum, Biscutella didyma, Diplotaxis erucoides, Neslia apiculata, Eruca sativa, Rapistrum rugosum, Calepina irregularis, Medicago orbicularis, M. hispida, Trifolium resupinatum, Hymenocarpus circinnatus, Vicia narbonensis, V. peregrina, Lathyrus marmoratus, L. annuus, L. erectus, Erodium malacoides, Malva nicaeensis, M. parviflora, Ammi visnaga, Heliotropium europaeum, Marrubium vulgare, Galium tricorne, Notobasis syriaca, Silybum marianum, Cichorium pumilum, Bromus scoparius, B. macrostachys, and *Gladiolus segetum.*

While the question of the primary "home" of the pluriregional segetals and ruderals cannot always be answered easily, there are reasons to assume that most of the Mediterrano–Irano-Turanian segetals are Irano-Turanian in origin. Firstly, not a single segetal species of this group has as yet been observed in primary habitats within the Mediterranean region, while some have also been found in primary habitats in the Irano-Turanian region. Besides, segetals are light-demanding species, and it is hardly feasible that they should have originated from the Mediterranean region, with its closed arboreal climax communities. Further comprehensive investigations along this line will, most probably, reveal that the Mesopotamian subregion, closest in its ecology to the Mediterranean, is the home of a large number of East Mediterranean and Mediterrano–Irano-Turanian weeds. It is also probable that the Irano-Turanian region is the primary home of a long series of Mediterrano–Irano-Turanian nonsegetal species that occur within the Mediterranean territories, in open communities, where the primary arboreal vegetation has been devastated by man.

Among the halophytic interregionals mention may be made of some species of *Suaeda, Salsola, Frankenia,* and *Salicornia,* as well as of *Cressa cretica, Sonchus maritimus, Sphenopus divaricatus,* and *Aeluropus littoralis.*

In conclusion, it must be emphasized that interregional groups, notwithstanding the important part they often play in a vegetation, particularly under specific edaphic conditions, do not by any means efface the phytogeographical characteristics of a region. The latter are substantiated by the uniregionals, which are the true phytogeographical expression of the region, however abundant its interregionals may be.

Plantgeographical Territories of Palestine

The analysis of the flora into its phytogeographical groups and the attempt to define the distribution of these groups within Palestine led Eig (1931–32) to divide Palestine into three phytogeographical territories: the Mediterranean, the Irano-Turanian, and the Saharo-

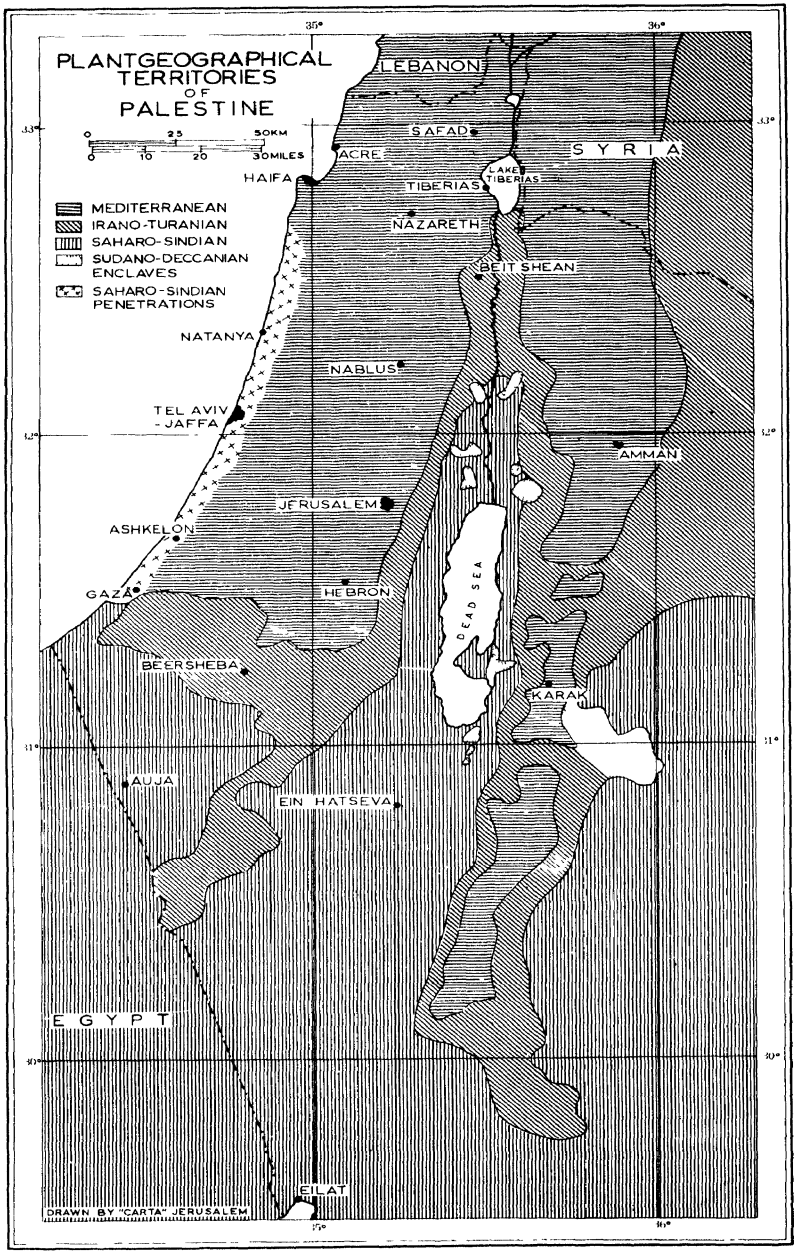
Sindian (Map 4). Each of these phytogeographical territories is characterized not only by its flora and vegetation but also by its climate and soils.

The Mediterranean Territory. This extends over a large part of Cisjordan and forms a belt of considerable width in Transjordan. Although readily recognizable by its flora and vegetation, its boundaries with the adjoining Irano-Turanian territory cannot be drawn with exactitude because the Mediterranean vegetation of the eastern and southern margins, which border on steppes and deserts, has been subject to heavy devastation by man. In consequence, plants from adjacent territories were able to penetrate into this border area to such an extent as to form a fairly broad transition belt of a mixed flora and vegetation in these borderlands.

In the north, this territory adjoins the Mediterranean part of Lebanon and Syria. In southern Cisjordan the limit of this Mediterranean territory runs along a line drawn from Gaza eastwards to Ruhama. Its eastern boundary passes in the mountains near the main watershed, east of Hebron, Jerusalem, and Nablus, and west of Tiberias. This territory also includes a large part of the northern Jordan Valley, as well as a long belt of the Transjordan Plateau, which extends as far south as the heights of Edom. The territory as a whole is characterized by a subhumid Mediterranean climate, but minor climatic variants can be distinguished according to topography, distance from the sea, and local differences in annual rainfall. The most typical soil variety is terra rossa, but rendzina, basalt, and sandy soils also occur. With the exception of the above-mentioned transition belt and certain other areas which are edaphically unfavorable for tree growth, the territory is generally characterized by forest and maquis climax communities.

The Irano-Turanian Territory. This occupies a comparatively narrow strip in Cisjordan, east and south of the Mediterranean territory. In Transjordan, it encircles the Mediterranean territory from south, east, and west and merges into the Syrian Desert in the northeast. Its climate is generally more continental, and the amount of annual precipitation varies from 350 to 200 mm. The rainy season is somewhat shorter and monthly rainfall is less evenly distributed than in the Mediterranean territory. The two main soil varieties of this region are gray steppe soil and loess. Vegetation comprises herbaceous and dwarf shrub communities, with almost no arboreal climax. Agriculture is very poor, unstable, and almost entirely confined to plains and valleys.

The Saharo-Sindian Territory. This is the largest of the three territories, occupying about half the area of Palestine. The bound-


PLANTGEOGRAPHICAL TERRITORIES OF PALESTINE
0 25 50KM
0 10 20 30MILES
MEDITERRANEAN
IRANO-TURANIAN
SAHARO-SINDIAN
SUDANO-DECCANIAN ENCLAVES
SAHARO-SINDIAN PENETRATIONS
LEBANON
SAFAD
ACRE
SYRIA
HAIFA
LAKE TIBERIAS
TIBERIAS
NAZARETH
BEIT SHEAN
NATANYA
NABLUS
TEL AVIV - JAFFA
AMMAN
JERUSALEM
ASHKELON
DEAD SEA
GAZA
HEBRON
BEERSHEBA
KARAK
AUJA
EIN HATSEVA
EGYPT
EILAT
DRAWN BY "CARTA" JERUSALEM
35°
36°
33°
32°
31°
30°
29°

Map 4.

aries it shares with the Irano-Turanian territory, however, are vague. The greater parts of Edom and the Negev, included within the area, are mere continuations of the Sinai on one side and of northern Arabia on the other. This territory has a typical desert climate with a short rainy season and a long, hot, and dry summer. The annual amount of precipitation varies from 200 to 25 mm. The main soil varieties are hammadas, sands, and salines. Vegetation is extremely poor and mainly confined to depressions, wadis, and ru mels. No successional seres occur and no arboreal climax communities are found here, except in hydrophytic and hydro-halophytic habitats. Agriculture is altogether lacking, except in oases or in flooded wadis.

The outlet areas of some watercourses into the lower Jordan Valley and the Dead Sea, with their higher winter temperatures, are the sites of a Sudanian flora and vegetation.

The light soil belt of the Mediterranean coastal plain is a penetration area for a considerable number of Saharo-Sindian species. Other penetration areas are the intensively cultivated great alluvial plains. These harbor, among others, numerous segetals of Irano-Turanian origin.

Most interesting is the deep penetration of some Irano-Turanian trees and shrubs into the Mediterranean territory in places where the primary forests have been depleted. Examples are *Zizyphus lotus, Pistacia atlantica, Prunus amygdalus*, and others.

Endemics

While the above analysis reveals the present plantgeographical make-up of the flora of Palestine, an analysis of its endemics may, with the aid of adequate taxonomic data, yield some suggestions as to the origin of, and degree of speciation in, certain taxonomic groups. In an area of so heterogeneous a plant geography and ecology, it may also reveal relations between environment and speciation.

The flora of Palestine includes 160 endemic species, i.e., 7.1 per cent of its total number of vascular plants. These figures are far from being final and may change considerably with the advance of taxonomic research in the area. This percentage is rather high as compared with that recorded for the flora of Syria or Egypt, but in comparison with that recorded for other East Mediterranean countries, such as Lebanon and Turkey, or for the Balkan Peninsula, it is very low. Turrill (1929), for instance, records as much as 26 per cent of endemic species for the Balkan Peninsula. One of the reasons for the small number of endemics in Palestine is, no doubt, its lack of alpine and subalpine elevations.

Palestine's endemics are dispersed over 30 of its 114 families, and no proportion exists between the size of the family and the number

of endemics. The Leguminosae family, for instance, with its 268 species, comprises 21 endemics, while among the 23 indigenous species of Iridaceae, 8 are endemic. In the Gramineae (198 species) 10 are endemic; in the Cruciferae (124 species), 9; in the Caryophyllaceae (97 species), 5; and in the Chenopodiaceae (60 species) the number of endemics is 4. There is not a single endemic among the 23 species of *Medicago* occurring in Palestine, while there are 12 among the 44 species of *Astragalus*. Of the 10 local *Crepis* species none are endemic, while 5 out of 10 *Onopordon* species are. Among the 13 indigenous species of *Iris* there are as many as 8 endemics, while there are none among the 15 species of *Bromus* or the 31 species of *Euphorbia*. Some species are significant in that they give rise to numbers of endemic varieties. Examples are *Quercus calliprinos*, *Q. ithaburensis*, *Polygonum equisetiforme*, *Erucaria myagroides*, *E. boveana*, *Matthiola longipetala*, *Retama raetam*, *Tamarix gallica*, *Aegilops peregrina*, and many others.

Relative Ages. Much stress has often been laid on the estimate of the relative ages of the endemics. Though such estimates have to be approached with caution, there are some objective criteria for the distinction between neo- and paleo-endemics. While the former are still connected with their progenitors, taxonomically or spatially or both, the latter are isolated both taxonomically and geographically. Most of Palestine's endemics are neo-endemics in the above sense. As an example of paleo-endemics *Daphne linearifolia* may be mentioned. It is found only in the heights of Edom and is distantly related to *D. acuminata*, occurring in Armenia, Kurdistan, Iran, Afghanistan, and Baluchistan and to *D. mucronata*, occurring in southern Europe, Asia Minor, Afghanistan, and the Himalayas. It is undoubtedly a relic of a Mediterranean and Irano-Turanian arboreal flora which invaded larger stretches of the present highlands of Edom, the Negev, and Sinai during one of the humid periods of the Pleistocene. When retreating in the succeeding period, this flora left behind relics in the more sheltered habitats. Such relics are, among others, *Pistacia palaestina* (in Arabia), *Juniperus phoenicea*, *Crataegus sinaica*, *Pistacia atlantica*, *Rhamnus disperma* (Sinai), and *Cupressus sempervirens*, *Prunus prostrata*, *Euphorbia thamnoides*, *Hedera helix* (Edom). It is probable that the following are also relic endemics of this invasion: *Polygala edumea*, *Alyssum dimorphosepalum*, *Trichodesma boissieri*, *Origanum dayi*, *Scrophularia nabataeorum*, and others.

Of interest are several groups of endemics confined to relatively limited areas. There are, for instance, six endemic species of *Tamarix* which are found only in the Jordan and Arava valleys. This, to-

gether with the fact that there is a high variability among the other species occurring here, suggests that this particular area, together with Arabia and southern Iran, constitutes a marked center of speciation in *Tamarix*, although smaller than that located in the Turanian subregion. Of similar interest are the seven very closely related endemic species of *Iris*, subgenus *Oncocyclus*. In spite of being spatially separated from each other, they are much alike in their ecological requirements, being confined to semisteppe or other open herbaceous communities. They are the southernmost representatives of this subgenus and may be looked upon as an example of marginal splitting ("Rand Abspaltung," Meusel, 1943). Their relatively recent formation is suggested by the fact that some of the species intergrade with one another and others intercross readily. Of the 12 endemic *Astragalus* species, 6 belong to section *Christiana* and represent the southernmost outpost of that section, which is limited to the East Mediterranean and Irano-Anatolian subregions. Their local distribution and their taxonomic interrelation suggest that they may be another example of more recent marginal splitting. Similar assumptions can be made with regard to the seven endemic species of *Anthemis*, of the affinity of *A. melampodina* and *A. cornucopiae* groups. From the three endemic *Centaurea* species of the relatively small section *Calcitrapa* and the array of endemic varieties within other species of that section, one may presume that its center of speciation is located in the southeastern corner of the Mediterranean region. Again the five endemic species of *Onopordon* occurring here lead one to the same assumption for the *Heteracanthum* group of that genus.

A number of local endemics show clear taxonomic relations to other sister species occurring in or outside Palestine. Examples are *Rheum palaestinum*, *Dianthus judaicus*, *Psoralea flaccida*, *Pimpinella petraea*, *Eremostachys transjordanica*, *Campanula hierosolymitana*, *C. aaronsohnii*, *Calendula pachysperma*, *Cousinia moabitica*, *Scorzonera judaica*, *Poa hackelii*, and *P. eigii*.

An interesting case is that of *Caralluma*, which is represented by two related endemic species and one endemic variety, all belonging to the *Boucerosia* group. One of them, *C. negevensis*, is a Saharo-Sindian species, another, *C. aaronis*, an Irano-Turanian species, while *C. europaea* var. *judaica* is Mediterranean. Another endemic species, *C. maris-mortui*, is of the *Lalacruma* group. All the species of *Caralluma* are without doubt relics of the Tertiary period during which tropical vegetation prevailed over most parts of Palestine.

A number of endemic species are coastal vicariads of corresponding taxa of the interior. Examples are *Polygonum palaestinum* (unpublished), *Paronychia palaestina*, *Scrophularia telavivensis*, *Galium*

lasianthum, Senecio joppensis, Echinops philistaeus, and *Allium telavivense.*

About half of Palestine's endemics are confined to the Mediterranean territory, about a third to the Irano-Turanian, and only a sixth to the Saharo-Sindian territory. Compared with the total number of species by which each of the above elements is represented in Palestine, the figure obtained for the Mediterranean element is 8.7 per cent, for the Irano-Turanian 16.5 per cent, and for the Saharo-Sindian 8 per cent. These figures no doubt show that the Irano-Turanian region is more favorable for speciation than the Mediterranean. This accords well with the fact that the Irano-Turanian region harbors an exceedingly large number of endemic genera and species. Many of the Mediterranean and Saharo-Sindian endemics are, most certainly, derivatives of Irano-Turanian stock. One can find examples in the genera *Astragalus, Ribes, Salvia, Eremostachys, Anthemis, Centaurea, Bellevalia, Iris,* etc.

In Palestine three larger centers of endemics can be outlined, namely, the coastal plain, notably its southern part, the Jordan Valley, and the highlands of Edom and the Negev. The 20 and more species endemic in the coastal plain are all Mediterranean neoendemics. The secluded position of the sector, which has Mount Carmel as its northern barrier and the Saharo-Sindian territory of the Negev isolating it from the south, is doubtless the reason for their concentration here. The Jordan Valley, with about 25 endemics, is enclosed by mountain ranges on either side and constitutes an isolated area with a subtropical to tropical climate. The highlands of Edom and the Negev, which are ecologically isolated from the surrounding deserts, harbor about 40 endemics. The remainder of the endemics are scattered throughout other parts of Palestine, notably the areas bordering different plantgeographical territories. Most of Palestine's endemics are confined to loosely populated plant communities. Noteworthy are those endemics which occur as more or less obligatory weeds, e.g., *Alkanna galilaea, Galium chaetopodum, Salvia eigii, Stachys zohariana,* and *Lachnophyllum hierosolymitanum* (unpublished).

Vicariism and Variation Patterns

The meeting of three plantgeographical regions within so limited a space, the diversity of ecologic sites within each of the plantgeographical areas, and the presence of so many species reaching their limits of distribution within Palestine are all facts accounting for the occurrence of polymorphy and particular variation patterns in the local flora.

A series of closely related species replace each other exclusively in two or more plantgeographical areas. An example of biregional vicariism is *Aegilops sharonensis,* confined to the Mediterranean coastal plain, and *A. bicornis,* replacing the former in the Saharo-Sindian territory. A few of the many examples of Mediterrano-Saharo-Sindian vicariads are *Maresia pulchella–M. pygmaea; Reseda alba–R. decursiva; Psoralea bituminosa–P. flaccida; Astragalus callichrous–A. maris-mortui; Erodium moschatum–E. deserti; Euphorbia peplus–E. chamaepeplus; Tamarix meyeri–T. deserti; Ballota undulata–B. kaiseri; Teucrium polium–T. leucocladum; Plantago squarrosa–P. maris-mortui; Plantago psyllium–P. chamaepsyllium; Galium judaicum–G. hierochuntinum; Senecio joppensis–S. coronopifolius;* and *Calendula arvensis–C. aegyptiaca.*

Mediterrano–Irano-Turanian vicariism is evident in the following pairs: *Nigella arvensis* var. *tuberculata–N. arvensis* var. *deserti; Glaucium aleppicum–G. grandiflorum; Erucaria myagroides–E. boveana; Lagoseris sancta–L. obovata; Picris amalecitana–P. intermedia; Calendula palaestina–C. pachysperma; Poa bulbosa–P. eigii* and *P. sinaica; Allium telavivense–A. aschersonianum; Fritillaria libanotica–F. arabica; Gagea dayana–G. tenuifolia;* and many others.

Irano-Turano-Saharo-Sindian vicariism manifests itself in *Anabasis haussknechtii–A. articulata; Astragalus palmyrensis–A. bombycinus; Heliotropium rotundifolium–H. maris-mortui.*

Examples of triregional vicariism are provided by the following triplets: *Caralluma europaea* (Mediterranean)–*C. aaronis* (Irano-Turanian)–*C. negevensis* (Saharo-Sindian); *Anthemis cornucopiae* (Mediterranean)–*A. hebronica* (Irano-Turanian)–*A. maris-mortui* (Saharo-Sindian); *Centaurea procurrens* (Mediterranean)–*C. negeviana* (Irano-Turanian)–*C. calcitrapella* (Saharo-Sindian); and a few others.

Intraregional vicariism brought about by differences in edaphic or microclimatic conditions is exemplified, among others, by the following pairs of Mediterranean species, with the first-named species in each case being limited to the light soils of the coastal plain and the second to the heavy soils of the hills and mountains: *Ononis stenophylla–O. natrix; Erodium telavivense–E. gruinum; Alkanna tinctoria–A. strigosa;* and *Allium telavivense–A. dumetorum.*

Ecotypic Differentiation

There is a series of species split into morphologically and ecologically well-defined races. Examples of species differentiated into littoral and inland ecotypes are the following: *Polygonum equiseti-*

forme, Beta vulgaris, Nigella arvensis, Papaver rhoeas, Verbascum sinuatum, Vaillantia hispida, Pallenis spinosa, Echinops viscosus, Lagurus ovatus, Koeleria phleoides, Lolium rigidum, and many others. The littoral ecotypes are often also characterized by certain specific features such as prostrate habit, succulence, or other genetically fixed characters.

Examples of species represented by both a desert and a non-desert ecotype are *Ranunculus asiaticus, Vicia narbonensis, Malva parviflora, Bupleurum subovatum, Plantago coronopus, Filago spathulata, Oryzopsis miliacea, Helicophyllum crassipes,* and many others.

There are also a series of species whose various strains differ only very slightly or not at all from one another in morphologic characteristics but exhibit differences in their behavior in regard to phenology, drought resistance, germination, etc. These differences are evidently genetically fixed. It is possible that a large number of species widespread in Palestine and apparently "monotypic" belong to this category, as a recently initiated comprehensive study on these lines may reveal (Waisel, MS.).

In many species, occurring at the limits of their distribution, variation manifests itself in a multitude of apparently non-adaptive characters. Such variations have been observed in *Quercus ithaburensis, Q. calliprinos, Capparis spinosa, Matthiola longipetala, Erucaria boveana, E. myagroides, Crataegus azarolus, Retama raetam, Trigonella monspeliaca, Astragalus tribuloides, Vicia angustifolia,* and many others. Further study is needed to ascertain the degree of genetic stability of these forms.

Little is known so far about hybridogenic variations in the local flora. Orthodox taxonomic methods do not succeed in detecting the hybrid forms as such. An interesting example of interspecific hybrids is furnished by the rare *Pistacia saportae,* a hybrid between an evergreen *Pistacia lentiscus* and a deciduous *P. palaestina.* There are also several hybrids among the local species of *Salix.* More recently natural hybrids between the following species have also been found: *Fumana thymifolia* and *F. arabica, Verbascum sinuatum* and *V. tripolitanum, Erigeron crispus* and *E. canadensis, Aegilops sharonensis* and *A. longissima,* etc.

Discontinuous Areas of Distribution

A considerable number of species of the local flora exhibit a striking discontinuity in their distribution area. Among others there are the following five types of discontinuity.

1. Tropical Discontinuity. Many tropical hydrophytes reach their northern limit of distribution in Palestine, where they form

isolated outposts widely separated from their main area. Examples are *Marsilia diffusa, Polygonum acuminatum, Cyperus lanceus, C. papyrus,* and *C. latifolius.*

2. Boreal Discontinuity. Another group of Palestine hydrophytes, mainly of Eurosiberian origin, have so far not been found either in Syria or in Turkey or in both. Examples of such species are *Dryopteris thelypteris, Nymphaea alba, Scutellaria galericulata, Utricularia vulgaris, Hydrocharis morsus-ranae,* and *Vallisneria spiralis.*

Both of these cases of discontinuous distribution can perhaps be explained by the location of Palestine on the main route of bird migration. Many of the above-named hydrophytes may have been brought in from distant countries by birds interrupting their flight in the aquatic habitats of the Huleh region and the coastal plain.

3. Omni-Mediterranean Discontinuities. A large number of plants regarded as Omni-Mediterranean do not occur in the southeastern corner of the Mediterranean region, that is, in Sinai, Egypt, Marmarica, and partly not in Cyrenaica and Tripolitania. This is true—to cite a few instances—of *Pinus halepensis, Juniperus oxycedrus, Cupressus sempervirens, Laurus nobilis, Ceratonia siliqua, Pistacia lentiscus, Rhamnus alaternus, Phillyrea media,* and *Viburnum tinus.* This Sinaitic-Lybian gap in the distribution of the Omni-Mediterranean element is very conspicuous and has its reasons in the climatic conditions of "gap" countries, where the North African desert closely approaches the Mediterranean seashore. It is most instructive to observe the gradual disappearance of many Omni-Mediterranean species in Palestine as they approach that gap from the north. Some of them cease to occur already in upper Galilee, e.g., *Juniperus oxycedrus, Arabis turrita, Geum heterocarpum, Antirrhinum majus, A. tortuosum,* and *Agropyron panormitanum.* Others reach their limits further south in Samaria, e.g., *Clematis flammula, Spartium junceum, Geranium lucidum, Rhamnus alaternus, Myrtus communis, Jasminum fruticans, Melica minuta, Ruscus aculeatus.* The majority, however, disappear only in the Judean Mountains, e.g., *Pinus halepensis, Clematis cirrhosa, Laurus nobilis, Pistacia lentiscus, Cistus villosus, C. salvifolius, Phillyrea media, Osyris alba,* and many others. The continuity in the distribution of some Irano-Turanian plants, such as *Pistacia atlantica, Rhus tripartita,* and *Zizyphus lotus,* is interrupted over the same area.

4. West Mediterranean Discontinuities. A few West Mediterranean species occurring in Palestine are separated by a wide gap from the western part of their area. Examples are *Melilotus italica, Coronilla repanda, Tetragonolobus requieni, Euphorbia dendroides,*

Chrysanthemum viscosum, and *Carlina racemosa*. One may perhaps regard these plants as relics of a larger group which inhabited the East Mediterranean countries in a more humid period of the Pleistocene and which, on retreating, left single species scattered here and there in Palestine or elsewhere in the East Mediterranean.

5. Irano-Turanian Discontinuities. Irano-Turanian species such as *Maresia pygmaea, Euphorbia cheiradenia, Scorzonera intricata, Aegilops crassa*, etc., occur in Palestine but have their next station far away from it. The presence of such species in discontinuous areas, together with the occurrence of certain endemics closely related to Irano-Turanians of somewhat remote districts, furnishes evidence for the assumption that in one of the more humid periods of the Pleistocene the Irano-Turanian element prevailed over much wider areas of Palestine than it does at present.

Other irregular distribution patterns within the Palestinian flora will probably be explained only after further advance in the floristic exploration of the region has been made. There is, for example, *Viscum cruciatum*. It is fairly common in many districts of Mediterranean Palestine but outside Palestine and Lebanon has been found only in Spain and Morocco. *Haloxylon persicum*, forming large stands in southern Palestine, has recently been found also in northern Arabia, but its links with Iran and Central Asia, where it forms the "Saxaul forests," are still unclear. No mention is made here of the many discontinuities in plants which may be classed as neophytes and which have been unintentionally introduced by man.

Origin of the Flora

In the preceding paragraphs a division of the flora into plantgeographical groups has been given, based on the recent regional distribution of species. It is indisputable that factors of this distribution are largely to be sought in the past history of the flora concerned. De Candolle (1855) went as far as to state in that regard that "les causes physiques et géographiques de notre époque ne jouent qu'un rôle très secondaire."

Historical Groups. To analyze a flora into its historical elements, that is, into groups of common origin and common migration routes, and to determine the periods of their arrival in the respective countries, requires a large body of paleobotanical and paleogeographical data. Much advance has been made recently regarding the history of floras of the Temperate Zones of the Northern Hemisphere through the studies of Kryshtofovich (1929), Reid and Chandler (1933), Edwards (1936), Chaney (1940), Barghorn (1951), Principi (1942),

and others. The Mediterranean and Near Eastern countries have been very slightly explored in this regard, so that a study of their floras from a historical viewpoint is based on the few relevant data as well as on findings and conclusions available for adjacent areas.

In the following, a preliminary attempt is made to point out some of the more prominent historical groups of Palestine's flora and to outline roughly the main local plantgeographical events of the Tertiary period that have led to the present make-up of the flora. It is generally assumed that changes of climate during the Tertiary manifested themselves in a shifting of the latitudinal belts into which the earth's climate was differentiated then, much as it is today. This latitudinal belting was, of course, largely deranged by geomorphologic events of the respective geological periods. Although floras have either reacted to such changes by mass migration or were rooted out, invading floras have not been able to eliminate totally the preceding indigenous ones. Remnants of older floras have always been able to escape extermination by occupying sheltered habitats or by developing biotypes tolerant to the changed conditions. As a result, the number of historical groups preserved in a continuously vegetated area shows some accordance with the climatic vicissitudes to which this area was subjected during the geologic past. Of the comparatively high number of historical elements occurring in the flora of this country as a result of its past climatic and floristic changes, only the following will be pointed out:

1. The Paleotropical Group. This is a very ancient element, mainly of Tropico-African stock. It played an important part in the flora of the Northern Hemisphere during the Cretaceous and Early Tertiary, and dominated the Mediterranean in particular. This element subsided with the decrease of temperature in northern latitudes, leaving remnants and derivatives. Examples are the genera *Ficus, Laurus, Ceratonia, Cercis, Myrtus, Styrax, Smilax, Tamus,* and many others.

2. The Sudanian Group. This comprises another old tropical element which probably dominated the southern Mediterranean during the Miocene and retreated in the Pliocene period. Remnants of that group have survived here in suitable habitats. Representatives of the genera *Capparis, Moringa, Acacia, Balanites, Salvadora, Zizyphus,* and *Caralluma* are examples.

3. The Arctotertiary Group. The Arctotertiary flora, which dominated the Northern Holarctis during the Early Tertiary, was driven southwards with the advent of a colder climate and was largely destroyed in western Eurasia. Some representatives of this

group took refuge in the Mediterranean region, although to a lesser extent than in the Colchico-Hyrcanian region. Examples are species of the genera *Pinus, Populus, Quercus, Ulmus, Platanus, Genista, Acer,* and others.

4. The Paleo-Saharian Group. While the bulk of the Saharo-Sindian flora is derived from the Mediterranean, Irano-Turanian, and Sudanian stock, it also has an autochthonous nucleus. Taxonomically more or less isolated genera, such as *Gymnocarpos, Anastatica, Zilla, Morettia, Gymnarrhena,* as well as a number of other genera belong to this group.

5. The South African Group. South Africa is the center of origin of a very large number of genera, today represented in the Mediterranean and the adjacent regions, e.g., *Aizoon, Mesembryanthemum, Corrigiola, Lotononis, Monsonia, Zygophyllum, Citrullus, Ifloga, Tripteris, Iphiona, Leyssera, Aristida, Androcymbium, Gladiolus, Ornithogalum,* and many others. The question of a migration of this group into the Mediterranean area and southwestern Asia has been widely discussed by Schmid (1946), Croizat (1952), Schwarz (1938), Nordhagen (1937), Popov (1927), and others. Opinions on this subject are still divergent.

6. The Turanian Group. Central Asia is generally assumed to have been an ancient center of xerophytic and halophytic floras. This center, referred to by Popov (1927), Kryshtofovich (1929), Grossheim (1936), and others, expanded considerably following the retreat of the ancient Tethys Sea from Asia. From here numerous halophytic and eremophytic species and genera spread both into the deserts of southwestern Asia and the Sahara, and into the littoral zones of the Old World (Iljin, 1946). Examples are found in the genera *Calligonum, Haloxylon, Salsola, Anabasis, Noëa, Tamarix,* and *Artemisia.*

7. The Irano-Anatolian Group. The large plateau extending between Afghanistan and the western margin of interior Anatolia represents a primary speciation center for yet another type of xerophytic flora, particularly of steppe plants characterized among others by the genera *Silene, Alyssum, Astragalus, Onobrychis, Ferula, Acantholimon, Phlomis, Salvia, Verbascum, Cousinia, Scorzonera, Centaurea,* and *Allium.* This xerophytic flora supplied a great number of specific and generic derivatives to the present Mediterranean region, which from the historical point of view is considered a secondary center of speciation (Schwarz, 1938). It has also given rise to a series of derivatives which have penetrated deeply into the Saharo-Sindian region.

Main Historical Events. The above are the most obvious historical elements that make up the local flora. They indicate the main centers of origin of this flora. The times of these elements' arrival in Palestine can be deduced only indirectly from analogies with neighboring countries that are richer in paleobotanical records. Thus the following outline of the main events in the history of the flora is essentially fragmentary.

THE CRETACEOUS. During the Cretaceous the greater part of Palestine was covered by the sea, while certain parts of Edom and the southern Negev constituted vast deserts. Paleontological findings, dating from that period in this country and in Egypt, point to a tropical climate (Hirmer, 1942; Chandler, 1954).

THE EOCENE. The ancient Mediterranean Sea (Tethys) retreated from Palestine and Syria only in the Upper Eocene, but it persisted as a broad water body extending eastwards to India and separating Palestine and Syria from the Eurasian continent (Arldt, 1919–22). In those days Palestine was closely linked with Africa and was still governed by a tropical climate. There must have been a vivid interchange of species with Egypt, which was inhabited by a tropical flora at that period, as is evident from its fossils (Hirmer, 1942; Kräusel and Stromer, 1924; Krausel, 1939; Chandler, 1954).

THE OLIGOCENE. During the Oligocene the geography and climate of the region did not change to any considerable extent. Paleobotanical findings in Egypt point clearly to the prevalence of a hot and humid climate, supporting a tropical wood flora, which may have resembled that characteristic of the Afro-Asian tropics of today. Chiarugi (1930) even maintains that this tropical region was not limited to Africa alone but embraced southern Europe as well.

THE MIOCENE. The Miocene period is perhaps one of the most important in the history of the local flora. The larger part of Palestine continued to be land. Tectonic movements, such as the lifting of the mountains and the formation of the Jordan rift, were taking place. The connection with Africa still existed (Arldt, 1919–22), and a rather broad sea arm of the shrinking Tethys still separated the southeastern from the northeastern countries of the Mediterranean. According to Koppen (1931), the Mediterranean countries were governed by a climate similar to that of Sudan or the Sahara, and central Europe by a temperate subtropical climate. That Palestine had a tropical climate at that period is borne out by findings in Egypt of 18 fossilized wood species, most of them dating from the Oligocene-Miocene and a few from the Miocene period (Hirmer, 1942). The fossilized woods, including *Palmoxylon* sp. and most

probably other as yet unidentified tropical species that were recently found in the Neogene of the northern Negev, support this assumption. Even in the northern Mediterranean countries, the number of tropical genera was still very high during the Miocene, according to Principi (1942) and Guyot (1948). Under these tropical conditions there was little room in the Palestine of the Miocene period for the Arctotertiary element. At best, there may have existed certain Mediterranean wood species derived from the Paleo-Tropical element, side by side with a Sudanian savannah flora. Some authors (Eig, 1931–32; Bodenheimer, 1935; Hart, 1891) assume that this Sudanian element made its appearance in Palestine during the Pleistocene. However, in accordance with the arguments brought forward, the author shares the opinions of Tristram (1884) and Reichert (1940) as to the Miocene being climatically the most favorable period for the occurrence of that flora in Palestine. This is because the vast deserts which have separated Palestine from tropical Africa could not have offered a free passage to this element (Picard, 1937) in post-Miocene periods. With the advent of the Pliocene and the gradual decrease of temperature, the tropical flora subsided and has finally become reduced to about 40 species, most of them confined to some enclaves of the Jordan Valley.

THE PLIOCENE. During the Pliocene times the climate of Palestine changed fairly rapidly, as did that of other Mediterranean and sub-Mediterranean countries. It is assumed by a great many authors who base their evidence on paleobotanical records that a climate approximating that of the present period came into existence then. According to Stojanoff and Stefanoff (1929), the Pliocene flora near Sofia comprises among others recent Mediterranean species, such as *Pinus halepensis, P. pinea, Cedrus libani, Cupressus sempervirens, Quercus vallonea, Pistacia terebinthus, Rhus coriaria, Arbutus andrachne,* and *Olea europaea.* Similar findings have been recorded from Italy and France (Principi, 1942), although some tropical genera there are still intermingled with true Mediterranean ones. With the complete retreat of the eastern arm of the Tethys, an open land connection was established between Palestine and the northeastern Mediterranean, while the connection with tropical Africa was broken by the extreme deserts of Sinai and Egypt.

These changes resulted in the opening up of new routes for the penetration into Palestine and Syria of a number of Mediterranean trees and shrubs of the Holarctic stock from Turkey, Cyprus, and the Aegean. That this flora could not have entered Palestine from North Africa in pre-Pliocene times is evidenced by the fact that a

series of trees belonging to this element, such as species of *Quercus, Crataegus, Rhamnus, Arbutus,* and many others, do not occur in Mediterranean North Africa, although they are common in the northeastern Mediterranean countries. The common occurrence in both Cyprus and Palestine of hundreds of Mediterranean species points to the migrations having taken place at a time when Cyprus was still attached to northern Syria, that is, it excludes the possibility of the migrations having occurred only in the Pleistocene era.

An influx into Palestine of Irano-Anatolian derivatives coming from Anatolia may have occurred at that era simultaneously with an influx of Turanian derivatives, which have infiltrated there by way of Iran and Arabia. The latter were mainly desert halophytes and psammophytes. This flora took possession of the areas which are now mainly Irano-Turanian and partly also Saharo-Sindian territories. It spread south through Edom, Negev, and Sinai to the North African steppes and deserts and from there north to Spain and the Canary Islands.

THE PRESENT PATTERN. The present plantgeographical pattern of Palestine territories must have been in existence at the end of the Pliocene, when the present vegetational structure was also established. In the Pleistocene, the complete rift valley of the Jordan was already in existence. Volcanic eruptions had covered large parts of the Golan, Hauran, and Galilee with lava. The coastal plain emerged from the sea and sand dunes were piled up along the coast. The large diluvial "Jordan Sea," which occupied the greater part of the Jordan Valley, dried up during the Upper Pleistocene and left two relic seas, the Lake Tiberias and the Dead Sea.

Various authors have tried to synchronize the northern glacial and interglacial periods with the pluvial and interpluvial periods of Palestine's Pleistocene. Picard (1937) has differentiated Pluvials A, B, and C, and corresponding Interpluvials, with Pluvial A having the highest amount of rain. According to Picard, no radical climatic changes occurred in these periods of the Pleistocene. The year was already divided into a rainy winter and a dry summer, and the changing element through the periods was the amount, not the season, of rain. Accordingly, the boundaries of plantgeographical territories may have shifted to the west and north at one period and to the east and south at another, but no substantial changes in the basic make-up of the flora and vegetation occurred. The Eurosiberian and the West Mediterranean plants mentioned in the last chapter may be looked upon as being remnants of major groups which entered Palestine in one or another humid period of the Pleistocene. Simi-

larly, the existence of a few steppe species amidst the Mediterranean vegetation suggests an interpluvial advance of the Irano-Turanian element into the present Mediterranean territory. An important event of the Pleistocene was the establishment of the flora and vegetation of the coastal plain, which was submerged up to that period. Far-reaching changes in flora and vegetation were caused by the appearance of man. The effects of his interference with the plant cover, directly and indirectly, are discussed in Chapter 9.

4

Structure and Development of Vegetation

Structure

The Vegetal Landscape, Past and Present. The vegetation of Palestine comprises a considerable number of types differing from each other in their outer appearance. These types must have been in existence before the advent of man. From the fragmentary remains which are present today, a rough picture may be drawn of the primeval vegetal mosaic in existence before man began exerting his destructive influence on it. The vegetal cover thus deduced comprised then, as today, a variety of plant formations ranging from dense forests to thin patches of desert herbs. These formations are briefly reviewed below.

CONIFEROUS FORESTS. Only a single *Pinus* species plays an important part in the forest vegetation of Palestine today, but it is admittable that the rather rare stands of *Cupressus sempervirens* and *Juniperus phoenicea* were considerably more widespread in the past than they are at present.

SCLEROPHYLLOUS OAK FORESTS AND MAQUIS. In the past this type must have dominated the larger part of the Mediterranean territory both on mountains and in intermountain valleys on red and white-grayish soils.

DECIDUOUS, BROAD-LEAVED OAK FORESTS. Of this type a high-mountain *Quercus boissieri* forest comprising a number of deciduous rosaceous trees should be distinguished from the Sub-Mediterranean *Quercus ithaburensis* forest, which is confined to less humid conditions and to lower altitudes. The latter has probably expanded since at the expense of the Mediterranean sclerophyllous and malacophyllous oak forests, which have been largely destroyed by man.

EVERGREEN PARK-MAQUIS. This consisted of scattered *Ceratonia* trees with lower shrubs filling the interspaces. This largely thermophilous type can be considered to have occupied larger areas of the coastal plain and the contiguous foothills, and to a great extent also the eastern escarpments of the Cisjordan mountains.

DECIDUOUS STEPPE-MAQUIS AND STEPPE-FORESTS. These communities were limited to the Mediterranean–Irano-Turanian borderland, and consisted in the main of widely scattered trees of *Pistacia atlantica, Crataegus azarolus,* and *Amygdalus communis* and shrubs of *Rhamnus,* with steppe and semisteppe dwarf shrubs in interspaces.

DECIDUOUS THERMOPHILOUS SCRUB. Predominantly *Zizyphus lotus,* this scrub was confined mainly to the mountain slopes facing the middle Jordan Valley. This type of vegetation covers a larger area today than it did then, for it has encroached upon the neighboring Mediterranean arboreal vegetation that was largely ruined during the course of history.

HALOPHYTIC FORESTS. These forests, made up chiefly of various species of *Tamarix* and *Suaeda,* must have occupied quite considerable flooded saline and marsh areas in the vicinity of the Dead Sea and the Arava Valley. This same type of vegetation also inhabited the salines of the coastal plain after its emergence from the sea.

RIPARIAN WOODS. Consisting mainly of various species of *Salix, Tamarix,* and *Populus euphratica,* these predominated the river banks of the lowlands, while woods of *Platanus, Salix, Fraxinus,* and *Ulmus* may have occupied the banks of mountain rivers.

SAXAUL WOODS. These woods, composed chiefly of *Haloxylon persicum,* were confined then, as they are today, to the interior desert sand dunes of southern Edom and the Arava Valley.

SAVANNAH FOREST. This type, consisting largely of thorny *Acacia* species, *Zizyphus spina-christi, Moringa aptera, Salvadora persica,* and other tropical trees and shrubs, was limited mainly to the lower Jordan Valley, the Dead Sea shores, and the Arava Valley. The stands of *Zizyphus spina-christi* and *Acacia albida,* as well as the patches of *Hyparrhenia hirta* found today in the southern coastal plain, also indicate the existence there of a vegetation reminiscent of an East African savannah.

MEDITERRANEAN BATHA AND GARIGUE. These communities are dominated by low and dwarf evergreen shrubs, such as species of *Cistus, Phlomis, Salvia, Satureja, Poterium,* and *Thymus.* Though these are widespread in all parts of Palestine's Mediterranean terri-

tory today, they had a more limited distribution in the primeval vegetation. Their primary sites were probably confined to areas where climatic and edaphic conditions did not allow the development of maquis and forests.

DWARF SHRUB STEPPES. These steppes, chiefly of *Artemisia herba-alba, Noëa mucronata, Helianthemum* spp., etc., were confined to gray steppe soil of Palestine's Irano-Turanian territory, with nearly the same boundaries as at present. It is highly probable that the plains and depressions exhibiting deep loess and sandy loess soils were dominated by a grass steppe characterized by species of *Stipa, Aristida,* and others.

STEPPES OF APHYLLOUS, BROOMLIKE SHRUBS. Represented by *Retama raetam* and *Periploca aphylla* communities, these occupied considerable stretches of the Judean Desert, the rocky escarpments facing the Jordan Valley, and similar habitats.

LEAF AND STEM SUCCULENT DWARF SHRUB FORMATIONS. Comprising a large series of plant communities, these once formed the outstanding type of desert vegetation in the Saharo-Sindian territory of the Judean Desert, the Negev, and Transjordan, as they do today. A series of plant communities of succulent halophytic dwarf shrubs (e.g., *Suaeda* spp., *Salsola* spp., *Atriplex* spp.) were of common occurrence in the lowland salines both in the Jordan and Arava valleys, and in the coastal plain. It is likely that their distribution range expanded or grew smaller repeatedly, according to climatic oscillations or edaphic alterations that occurred in the past.

RUSH AND REED VEGETATION. This has always occupied swamps and river banks, both in the coastal plain and in the Jordan Valley.

* * *

The above vegetation types, conditioned as they are by gross climatic and edaphic factors, could not have changed considerably during the last geologic period. They may have repeatedly altered their extent and may have lost or gained certain of their components several times over as a result of minor oscillations in climate and geomorphologic surface developments which, however, did not affect their very existence and permanency.

Man as an Ecological Factor. Far-reaching changes in the distribution and make-up of a part of Palestine's vegetation began to take place only from that time when man became a major ecologic factor. Farming, pasturing, and industry resulted both in destruction

of existing types and invasions by alien ones. The outcome of man's activities on vegetation through the ages can be summed up as follows:

1. Destruction of natural vegetation occupying large stretches of alluvial soils in the coastal plain and the intermountain valleys. These low-lying areas have been under more or less continuous cultivation since very ancient times.

2. Destruction of the primary vegetation through cultivation, followed by abandonment of the cultivated area, often resulted in reoccupation of the area by a secondary climax vegetation. An example is the belt of the sandy clay soils of the Sharon Plain, which was abandoned by agriculture after having been under cultivation once or several times. No subsequent re-establishment of the supposed primary type of evergreen maquis occurred. Instead, the area became occupied by a secondary Sub-Mediterranean deciduous forest which was again destroyed and superseded in turn by a subtropical savannah grass steppe.

3. The immigration of an alien weed vegetation brought about by agriculture. Over 400 species of the local flora are obligatory or facultative weeds, a great part of which may be assumed to have their origin outside Palestine.

4. Changes in composition. Most of the prevalent plant communities, including those of the desert, have lost certain associates as the result of ever-recurring uprooting, burning, cutting, and overgrazing. In the ARTEMISIETUM HERBAE-ALBAE, for instance, many grasses have disappeared or become exceedingly rare. Similarly, the present composition of the evergreen maquis of *Quercus calliprinos* is certainly no more than a residue of a primary community from which those arboreal associates that could not withstand eradication and burning were eliminated.

5. Changes in dominance. Even in such communities where primary composition was not affected, frequency and dominance of the respective associates have altered greatly as a result of excessive use of certain plants by man.

6. Range extension. Many plant communities have expanded considerably beyond their former range of distribution and spread over contiguous areas cleared of vegetation by man. An example is the *Zizyphus lotus* scrub, which invaded large areas of the *Quercus ithaburensis* climax areas in lower Galilee. Another instance is the spreading of the batha and garigue communities over all areas originally occupied by forests and maquis. As a rule, range extension proceeds mostly in a one-way direction, that is, from xeric to more mesic habitats.

Reconstructing Vegetation. The ways and methods by which man introduced changes in the vegetation are legion, and the extent of these changes is not always conceivable. Hence, any attempt at reconstructing ruined or destroyed vegetation can be no more than an approximation. Some means of reconstructing devastated vegetation will be described briefly.

One of the most reliable sources of information concerning original vegetation is nature itself. Despite his destructive activities through the millennia, man has not succeeded in breaking nature's vigor and supremacy. His primitive tools and methods of cultivation and destruction have been inefficient in that they have not achieved a complete rooting out of the local vegetation. Pasture, axe, fire, and plough have done their part up to a certain limit, but at least small remnants of the former plant cover have been left here and there, against man's will and intention. These remains, negligible as they may sometimes seem, are valuable tools in the hands of experienced observers. Generally they consist of small woods, of groups of trees or shrubs, or even single specimens, which give testimony of the past nature of vegetation for entire provinces.

When attempting to clear vegetation in the mountain region, the primitive farmer faced two insurmountable obstacles: rocky ground and the regenerative vigor of the plant cover. Most of the Mediterranean mountain soils overlie hard rock and dolomites, which makes preparation of arable land by freeing it of trees exceedingly difficult. Here man has fought bitterly to eradicate deep-rooting trees and shrubs, but his efforts have been without success. Almost all trees and shrubs of maquis and forest are able to regenerate from subterranean stems and suckers, and this saved many woody plants from total destruction. It is for these reasons that one may find ineradicable shrubby oaks scattered here and there in the middle of a field on cultivated mountain terraces.

There is an Arabic proverb, "Trees never err." This means that trees are reliable indicators and that even a single tree, growing in a vast, desolated, woodless area testifies to the forests that previously existed in the area. While trees provide the most obvious clues for reconstruction of the vegetation, smaller vegetal remains such as stunted lianes or dwarf shrubs, or even certain moss species hidden in rock crevices, can give clear hints as to the nature of past vegetation in a particular area. In fact, students of vegetation in such areas are sometimes forced to apply archeological methods in deciphering the foregone vegetal landscapes.

Furthermore, there are the trees which man himself has intentionally left scattered here and there over the whole region, as an expres-

sion of certain religious habits. Deification of trees has been practiced from time immemorial and has been upheld by all peoples. Beneath trees men have "sacrificed and burnt incense," and buried their beloved and admired. These burial habits have remained a common practice up to the present day. The "sacred woods," so common an occurrence in the Near East, are reliable landmarks in the reconstruction of a ruined environment. Such carefully guarded and untouchable groves or single trees provide first-hand information not only of the previous existence of woodland in now devastated areas, but also of the probable composition of climax communities. The "sacred groves" and "holy trees" found in upper Galilee, on Mount Carmel, in the Judean Mountains, Transjordan, Syria, and Turkey bear witness to the past natural splendor and beauty of a landscape extremely barren at present.

Farmers and other landowners have often left single trees standing in their fields to provide shade and shelter against the burning sun or because of their edible fruit (e.g., carob trees, almond trees, hawthorn shrubs, wild pear trees, Christ's-thorn shrubs, and others). Wild fruit trees have been preserved to the present day in the most intensively cultivated parts of Syria and Turkey. For similar reasons, odd trees have been left untouched by axe and fire in great towns (Jerusalem, Hebron, and elsewhere).

In addition to these living pieces of evidence, there are countless scriptural and documentary data on the distribution of forests and trees in the past. In this connection the Papyrus Golinishef (eleventh century B.C.) may be mentioned, in which there are clear indications that Tantura (the ancient Dor) served as a harbor from which woods cut on Mount Carmel were exported to Egypt. Similarly, the accounts of Pliny, Flavius, and other historians and the narratives of early pilgrims, Crusaders, and other travelers are valuable sources of information as to the vegetal features of the country at the time of of their respective visits. Even recent documents such as the maps of the Palestine Exploration Fund, published in the eighties of the last century, supply evidence in this respect because they indicate forests in areas where only single trees are found today. From the Bible, the Mishna, and the Talmud, which are not concerned with natural vegetation as such, a certain amount of information can also be obtained regarding previous distribution ranges of certain indigenous trees and other plants.

Apart from the above methods, there is an indirect method of ecologic analogy which correlates vegetation to environment. By comparing the climatic and edaphic features of localities in which natural vegetation is still preserved with those prevailing in de-

forested areas, an approximate picture of the original vegetation may be obtained.

None of these means are fully adequate and in view of Palestine's long history of cultivation, conclusions have to be drawn with some reserve. Reconstruction of the primeval vegetation thus presents many problems which are still to be solved. Some of them will be discussed in the following paragraphs.

Vegetation Dynamics

Types of Plant Communities. From the developmental point of view, the local vegetation can be subdivided into the following categories: (1) climax communities, successional and non-successional, (2) sub-climax communities, successional and non-successional, and (3) seral communities leading to climaxes and to subclimaxes.

CLIMAX COMMUNITIES. These are relatively stable vegetation units which are in full equilibrium with the present-day climate and the ultimate developmental stage of the soil as conditioned by this climate. They show the highest competitive abilities under the governing physiographic conditions, and cannot develop further unless essential climatic-edaphic changes occur in their respective habitats. That the edaphic factor must not be underestimated in this regard is demonstrated by the occurrence of different climax communities on various soils governed by the same climate and by the fact that generally climate is unable to obliterate soil differences which originate from various rock formations.

Successional climax communities are the forests and maquis of the Mediterranean territory. They mostly reach their climax stage only after successional development, whereas garigue and batha formations, which are generally seral communities, may constitute a climax stage in the Mediterranean–Irano-Turanian borderland without earlier successional stages. In the Irano-Turanian and Saharo-Sindian territories most of the climax communities are on the whole non-successional, e.g., ARTEMISIETUM HERBAE-ALBAE, SUAEDETUM ASPHALTICAE, and ZYGOPHYLLETUM DUMOSI.

SUB-CLIMAX VEGETATION. According to Tansley (1939), the term "sub-climax vegetation" denotes temporarily stable vegetation units, conditioned by special factors which detain the development of the vegetation at a stage inferior to the potential climax of the area. When the detaining factors—which may be edaphic, physiographic, or biotic—cease to act, the development of vegetation proceeds in a direction toward the climax. So, for instance, the halophytic, hydro-

phytic, and psammophytic vegetation within the Mediterranean territory constitute sub-climax communities. These are apt to develop into the wood climax characteristic of the area after the specific restrictive soil factor is eliminated. The Huleh swamps are located within the climax area of the *Quercus ithaburensis* forest, but periodical flooding impedes the vegetation in its advancement toward that potential climax. The maquis of the typical subhumid Mediterranean habitats illustrate the case of a biotic sub-climax; the continuous destructive activities of man and his goats prevent this vegetation from developing into forest. Segetal vegetation is a further example of a biotic sub-climax.

SERAL PLANT COMMUNITIES. Within the Mediterranean territory seral plant communities are much more common than the corresponding climax and sub-climax communities. The leading seral plant associations preceding forest and maquis climaxes here are: POTERIETUM SPINOSI, THYMETUM CAPITATI, CISTETUM VILLOSI and C. SALVIFOLII, CALYCOTOMETUM VILLOSAE, SATUREJETUM THYMBRAE, PHLOMIDETUM VISCOSAE, and others. These comparatively long-lived communities are often preceded by annual or perennial short-lived pioneer associations. The following sequence illustrates seral succession from abandoned fields in the Judean Mountains toward the climax of evergreen *Quercus calliprinos* maquis or forests.

1. The pioneer community consisting of segetal plants led by the *Ononis leiosperma* and *Carthamus tenuis* holds the abandoned field for two to three years.

2. A hemicryptophytic assemblage of plants dominated by a series of grasses, such as *Hordeum bulbosum, Dactylis glomerata, Oryzopsis holciformis,* and others occupy the area for a short time.

3. The next stage is that of the POTERIETUM SPINOSI, which is dominated largely by the thorny dwarf shrub *Poterium spinosum.* The duration of this stage depends chiefly on the availability of seeds of garigue shrubs in the neighborhood, e.g., seeds of *Cistus villosus, C. salvifolius, Salvia triloba, Calycotome villosa,* and others. These may germinate in the interspaces left by *Poterium* or in the shade of this shrub and its associates. The seedlings can then enjoy the higher soil moisture afforded by virtue of the cover of the *Poterium* community.

4. As soon as garigue shrubs have become established on the spot they outgrow the *Poterium* shrubs and suppress the latter by robbing them of light and probably also of soil moisture. Sooner or later the *Poterium* community is replaced by one of the garigue communities. Seed availability is certainly not the only factor determining this succession.

5. While up to this point all stages of the succession have been observed directly, its further course toward the establishment of arboreal associates of the climax community so far has not been traced. But there is indirect evidence that trees and higher shrubs subdue the photophilous shrubs of the garigue community and gain a dominant position on the respective site.

For reasons not fully understood, forest and maquis climax communities require long periods for their re-establishment. During a time span of ten years, for example, the author failed to find a single tree specimen of the maquis starting to develop within undisturbed garigue communities, although seed supply of *Quercus calliprinos* and *Pistacia palaestina* was abundant in the nearest vicinity. Investigations are now under way as to the reason for these delays in the establishment of the last stage of the successional sere.

The sere leading to the QUERCETUM ITHABURENSIS climax is quite different from that described above. Neither *Poterium* nor *Cistus* participate in it. *Phlomis viscosa* and *Calycotome villosa* communities seem to play some part in the succession leading to the climax.

In the sandy soils of the Mediterranean coastal plain one can distinguish between five types of vegetation with regard to their successional dynamics: (a) The spray association of *Sporobolus arenarius–Lotus creticus* is a non-successional sub-climax community inhabiting steep slopes of the coast, which are exposed to salt spray. (b) The *Ammophila arenaria* community also represents a non-successional sub-climax able to withstand spray and onblow sands. (c) The *Artemisia monosperma–Cyperus mucronatus* community inhabits semiconsolidated dunes at some distance from the shore. Where the dunes become stable, as in the Sharon Plain, the latter is (or was in the past) superseded by the CERATONIETO-PISTACIETUM as a climax community. Sudden storms, however, or disturbances in the equilibrium of resting dunes brought about partly by man's activities may result in a destruction of the climax and the reoccupation of the dunes by communities of earlier successional stages.

FURTHER PROBLEMS. These are only a few known instances of vegetation dynamics within the Mediterranean territory. Much is still left to be investigated in this field. A few further problems that have bearing are now discussed.

First there is the regeneration and the rehabilitation of forests and maquis. It has already been stated that abandoned fields amidst the Mediterranean woodland do not become reoccupied by trees for a long period, despite abundant seed supply. Reasons for that delay are to be sought in the difficulty with which forest trees regenerate from seeds on exposed sites. Moisture supply is inadequate here

and young seedlings are probably unable to withstand summer drought in their first year. Since germination and seedling establishment are possible only under the canopy of trees preserved at the edge of cleared plots, revegetation by trees of even a small mountain terrace seems to be a matter of several generations.

A much graver problem is the re-establishment of the woody climax in the border belt of the Mediterranean region. Here, under the prevailing climatic conditions, the restoration of woods is hindered by the rapid soil erosion and desiccation which take place after the woods have been destroyed. In this border zone the land deprived of its woods sooner or later becomes occupied by steppe vegetation moving in from the immediate vicinity. This process has led to a considerable shrinkage of Mediterranean woodland areas, as evidenced by the occurrence of very old forest trees that are scattered in barren areas far away from the present woodland border. The island-like isolated stands of *Quercus calliprinos* and *Crataegus azarolus* in Jebel Druze, southeastern Syria, in a wide timberless area where tree growth is hardly feasible, are a case in point. Similar instances are a group of aged *Cupressus* trees in the highlands of Edom; the old trees of *Juniperus phoenicea* in Jebel Jelleg in the middle of the bland Sinai desert; imposing specimens of *Pistacia atlantica* in eastern Transjordan, the Syrian Desert, and the Negev Mountains, growing in a surrounding of vast deserts or steppes; or the old *Quercus calliprinos* trees in Wadi Waran, Transjordan. Similar traces of past woods are found on the margins of the Sahara and of other deserts that border on woodland. All these indicate bygone forests in areas where tree growth is entirely impossible today. Since the trunks of such trees are, as a rule, offshoots that have sprouted from age-old stumps, not even a rough estimate of the period in which these forests flourished can be made. Such trees may be likened to living fossils telling the story of the past without disclosing present and future potentialities of the area.

A reversion to such former climaxes is out of the question unless conditions for considerable soil improvement are created, which is beyond the scope of a mere passage of time. Changes in climate, however, such as a slight increase in the annual amount of rainfall, could compensate edaphic conditions considerably or might eventually lead to soil regeneration. Such slight climatic changes which may have occurred sporadically or in more or less orderly cycles within the prehistorical and historical past, as shown by Brooks (1949) and Murray (1951), are doubtlessly decisive in the regeneration of the discussed wood climaxes.

While the above is true for marginal climaxes, it seems that rehabilitation of wood climaxes within the optimal life zones of the Mediterranean region is a matter of time alone. Yet even in these zones one must be aware of the possibility that a particular wood community found today and usually considered a climax does not necessarily represent the potential ultimate stage of succession. A case in point is the forest of *Pinus halepensis* occurring here and there on white-grayish rendzina soils within the zone of broad-leaved maquis and forest. As will be pointed out in the next chapter, this pine forest should be regarded as a secondary climax. Another case is presented by *Pistacia atlantica* stands in the Huleh Plain and vicinity that are not the remnants of a *Pistacia* forest climax but alien intruders into ruined local woods. The probability that the *Quercus ithaburensis* forest of the Sharon Plain is not a primary climax in that area has been mentioned above. Restoration of climax communities during historical times could have taken place only where cultivated land had been abandoned and left undisturbed and thus exposed to revegetation for long periods. That this actually happened is evidenced by the fact that remains of human culture, such as wine and olive presses, cemeteries, and even remnants of olive groves are quite frequently found in sites covered today by fairly dense forests, as, for instance, in the environs of Alonim, lower Galilee. It is doubtful, however, whether the present floristic composition and range of such restored forest and maquis climax are entirely identical with those prior to man's intervention.

In the steppe and desert parts of Palestine one is confronted with questions not unlike those we have just discussed. The expansion of xeric vegetation into cleared, relatively mesic habitats of nearby territories is a common feature in Palestine. Ruin of steppe vegetation leads to the area's being invaded by desert vegetation. One can thus hardly rely on present boundaries between these two types when assessing the potential climax of the respective areas. In extreme deserts where soil profile development is almost non-existent, climaxes are generally non-successional in the conventional sense of that term. A destroyed ZYGOPHYLLETUM, for instance, may re-establish itself immediately in rainy years when sufficient moisture permits the seedlings to overcome the summer drought in their first year. Once established, dominant plants hold the site for very long periods and there is little chance for the development of additional seedlings in an adult stand, unless older members die off.

Untouched desert vegetation is extremely stable and sluggish. Sites once conquered by a particular plant community are held by it

for good, even if certain factors become subject to changes wrought by time. An example is furnished by *Artemisia monosperma*, which occupies onblow sands on loess but also remains growing on its site after the sand cover is blown off.

Steppe and desert plant communities are exceedingly poor in components. Each community is dominated only by one or a few evergreen chamaephytes, constituting its permanent framework. Since annual associates are ephemeral and develop in rainy years only, they are an unstable element here. Ten to 20 per cent coverage by permanent components makes the community saturated in the sense that it offers resistance to alien intrusion. The factor decisive in keeping contiguous communities apart from each other is without doubt the competitive root vigor of the respective dominant plants. So far, however, little is known about the nature and ecology of the competitive processes.

The present composition of desert plant communities in Palestine, as elsewhere, has to be looked upon as the outcome of a long process of selection of plants able to withstand the diversities of grazing and fuel collecting by man. Even where these activities cease, previous vegetation does not re-establish itself for long periods. For instance, areas of ARTEMISIETUM HERBAE-ALBAE that have been subject to overgrazing or cultivation continue to be dominated by secondary components, such as *Asphodelus microcarpus* or *Noëa mucronata*, for long periods after pasturing and cultivation on them have ceased.

Vegetation Classes

The concept of a plant community has been variously comprehended by various authors. Different schools of plant sociology have applied different methods for describing vegetation and have suggested various definitions of its basic units. A survey of the ample literature dealing with that subject is not within the scope of this volume. For methodologic material on the subject and criticism of current methods the reader is referred to Du Rietz (1921, 1931), Braun-Blanquet (1951a, 1951b), Gams (1954), Schmid (1954), Dice (1952), Cain (1932, 1939, 1944), Gleason (1929, 1939), Nichols (1930), Ashby (1935), Conard (1939), Goodall (1953, 1954), Oosting (1956), Rübel (1933), Whittaker (1951), and Dansereau (1957).

In spite of divergent opinions adopted by various schools as to fundamental concepts and the different methods, a considerable part of the world's vegetation has been investigated and classed into units that are quite comparable with one another.

In the following we have adopted the methods and concepts of the Zürich-Montpellier school led by Braun-Blanquet (1951a), according to which the basic unit of vegetation is the association. This is marked by its floristic composition, its peculiar characteristic species, its ecology, its dynamics and geography. Associations which show affinities in their floristic composition and ecology have been grouped together into alliances. This category has its practical uses, especially in mapping vegetation. Each alliance has its characteristic leading species often common to all associations included within it. It is often clearly defined by its gross habitat features. Along the same principles, alliances are grouped together in orders which are often marked by particular physiognomic traits. A still higher category comprising several orders is a class. This is also designated by the plantgeographical peculiarities of its components.

The following survey of plant communities is based on a large number of partly tabulated field records collected during two decades in almost all parts of Palestine. Many of the names of associations have been adopted from Eig (1939, 1946).

The natural vegetation cover of Palestine can be divided into the following 13 classes (M. Zohary, 1955).

Class of Quercetea calliprini. This comprises all Mediterranean forests, maquis, garigues, and bathas (dwarf shrub formations). It is subject to a Mediterranean climate, with a minimum annual rainfall limit of 350 mm. The QUERCETEA CALLIPRINI is found mainly on terra rossa and to a lesser extent on humiferous rendzina and consolidated sandy soils or sandstone. It is the class comprising the largest number of associations and it includes the largest part of the local flora. The following are some leading or dominant species of various associations characteristic of this class: *Pinus halepensis, Quercus calliprinos, Q. ithaburensis, Pistacia palaestina, P. lentiscus, Ceratonia siliqua, Laurus nobilis, Calycotome villosa, Cistus villosus, C. salvifolius, Phlomis viscosa, Satureja thymbra, Salvia triloba, Poterium spinosum, Thymus capitatus, Fumana thymifolia, Salvia graveolens, Ononis natrix, Echinops viscosus, Ballota undulata,* and *Carlina involucrata.*

Over half the area occupied by the QUERCETEA CALLIPRINI is taken up by these and several more leading species

This class is also well represented in other countries of the East Mediterranean subregion, e.g., Lebanon, Syria, and Turkey.

Class of Varthemietea iphionoidis. This class comprises the vegetation of rocks and rocky outcrops, walls, stone fences, and heaps

of rubble or gravel within the Mediterranean territory. Some of the plant communities of this class are confined to stone walls of human dwellings and others are pioneer communities. The dominant and most widespread species of this class are *Varthemia iphionoides, Podonosma syriaca, Stachys palaestina, Ballota rugosa, Micromeria serpyllifolia, Hyoscyamus aureus, Capparis spinosa, Umbilicus intermedius,* etc., as well as lichens and mosses. The only feature common to all these habitats is their stony substratum; in other respects they differ greatly from one another. Accordingly, this class is very heterogeneous in its vegetation and to some extent artificial. Three ecologic types may be distinguished here: true lithophytes, chasmophytes, and rubble-heap plants. The vegetation of this class is very striking in the landscape because it mostly includes poorly vegetated, rocky and stony ground. It has also been observed in other East Mediterranean countries.

Class of Retametea arenaria. This comprises several Mediterranean or Saharo-Sindian communities inhabiting mobile or fixed sand dunes, sandy clay plains, and the calcareous-sandstone hills (kurkar) all along the Mediterranean coastal plain. The particular climatic conditions, the vicinity of the sea with its salt-water spray, and the effect of the specific properties of sandy soil are responsible for an occurrence of series of plant communities, comprising, among others, about 150 species not found elsewhere in the country. The leading or most characteristic species of the various associations are *Ammophila arenaria* ssp. *arundinacea, Agropyron junceum, Lotus creticus, Sporobolus arenarius, Cyperus mucronatus, C. conglomeratus, Retama raetam* var. *sarcocarpa, Artemisia monosperma, Polygonum palaestinum, Silene succulenta, Ononis stenophylla, Convolvulus secundus, C. lanatus, Medicago marina, Tamarix gallica, Desmostachya bipinnata, Aegilops longissima, Aristida scoparia, Pennisetum dichotomum, Helianthemum ellipticum,* and others.

Class of Artemisietea herbae-albae. This class comprises the entire vegetation of the Irano-Turanian territory, growing on gray steppe soil and loess mostly with very shallow *A-C* or *C* profiles. At times it also occurs on hammada-like plains. The leading plants of the majority of its associations are dwarf shrubs and only a few are trees and shrubs. Its most characteristic plants in Palestine are *Pistacia atlantica, Zizyphus lotus, Retama raetam* var. *raetam, Phlomis brachyodon, Rhus tripartita, Artemisia herba-alba, Noëa mucronata, Anabasis haussknechtii, Haloxylon articulatum,* and *Achillea santolina.* A series of plant associations of this class are also

widely distributed in the steppe belt of North Africa, the Syrian Desert, and Iraq.

Class of Anabasidetea articulatae. This comprises the Saharo-Sindian communities characteristic of extremely dry and often saline hammada soils, as well as of gypseous and rocky desert ground. It is represented in the Negev, Edom, and in the lower Jordan Valley. The dominant life forms of the vegetation are therophytes—as well as xerophilous, mostly succulent chamaephytes. Leading species of the various communities are *Zygophyllum dumosum, Gymnocarpos fruticosum, Chenolea arabica, Salsola villosa, Atriplex parvifolia, Reaumuria palaestina, Suaeda asphaltica,* and *Anabasis articulata.*

Class of Haloxylotea salicornici. This is another class of Saharo-Sindian vegetation, confined to interior sand dunes and sandy plains, as well as to substrata of sandstone and granite. In Palestine it occupies parts of the Arava Valley and adjacent districts but also occurs in Arabia, Egypt, and southern Iraq. Among others, *Haloxylon persicum, H. salicornicum, Calligonum comosum,* and *Zilla spinosa* are most characteristic of this class.

Class of Acacietea raddianae. This class is represented here by a number of tropical plant communities. It is confined almost exclusively to wadis, notably outlet regions of the permanent and ephemeral watercourses of the Arava Valley, the lower Jordan Valley, and the Dead Sea shores. The leading plants are *Acacia raddiana, A. tortilis, Zizyphus spina-christi, Salvadora persica, Moringa aptera, Balanites aegyptiaca,* and *Calotropis procera.* The tropical species are often found associated with Saharo-Sindian ones.

Class of Suaedetea deserti. This class, which is characterized by a fairly large number of plant communities, comprises salt marsh vegetation of the Saharo-Sindian territory, i.e., in the Jordan and the Arava valleys, and in the vicinity of the Dead Sea. Ecologically it is related to the SALICORNIETEA FRUTICOSAE class, mentioned below, but differs from it in including a series of exclusive species and genera such as *Suaeda monoica, S. forskalii, S. palaestina, S. vermiculata, Salsola rosmarinus, S. tetrandra, Atriplex* spp., *Nitraria retusa, Tamarix* spp., *Tetradiclis salsa,* etc. Outside Palestine, this class is amply represented in Arabia, Egypt, Iraq, and Iran.

Class of Salicornietea fruticosae. This comprises the halophytic vegetation of the Mediterranean coastal plain. The characteristic species of the associations included in this class are *Tamarix meyeri,*

Arthrocnemum glaucum, Suaeda splendens, Salsola soda, Salicornia herbacea, S. fruticosa, Obione portulacoides, Statice limonium, Plantago crassifolia, Aster tripolium, and *Ipomoea sagittata.*

Class of Rudereto-Secalinetea. This class, which has been divided recently by Braun-Blanquet and others (1952) into several further classes, comprises the segetal and ruderal vegetation of Palestine in its entirety. It will be dealt with in greater detail in Chapter 9, "Man and Vegetation."

Classes of Hydrophytic Vegetation. One of these is the POTAMOTEA, comprising mainly floating plants of ponds and rivers. The other, the PHRAGMITETEA, consists of reed and rush communities, and the third, the POPULETEA, comprises the riparian tree and shrub vegetation. These classes are composed of a fairly large number of plant communities, some of which show geographical links with the Eurosiberian, others with the Mediterranean or tropical vegetation.

5

Mediterranean Wood and Shrub Vegetation

Forests, Maquis, Garigues, and Bathas (Quercetea calliprini Class)

Forest and Maquis (QUERCETALIA CALLIPRINI Order). The term "forest" does not require a definition from the physiognomic point of view; the name "maquis" conventionally denotes Mediterranean woodland dominated by sclerophyllous evergreen low trees and shrubs up to a height of 4 m. or so. As a rule, the maquis is composed of two or three layers of vegetation, among them some vines. The question whether the maquis represents a climax formation or a preclimax stage likely to develop into forest when undisturbed by man should be answered as follows: under favorable ecologic conditions and in the absence of human interference, maquis may develop into forests that are dominated by one or more tree species. This is demonstrated by the fact that most of the arboreal components of the maquis grow into handsome trees, when under protection. Thus evergreen forest and maquis cannot always be differentiated clearly, and will therefore be treated as a single unit.

Although the maquis is evergreen in general appearance, only about half the number of its tree species are evergreens. These are *Quercus calliprinos* (Fig. 10), *Pistacia lentiscus, Ceratonia siliqua, Phillyrea media, Arbutus andrachne* (Fig. 11), *Laurus nobilis, Rhamnus alaternus,* and others. Of the conifers *Pinus halepensis* is very common, while *Juniperus phoenicea, J. oxycedrus,* and *Cupressus sempervirens* are rare or confined to isolated spots only. Among the winter deciduous species are *Quercus ithaburensis* (Fig. 12), *Q. boissieri* (Fig. 13), *Pistacia palaestina, Styrax officinalis*

Fig. 10. *Quercus calliprinos.*

(Fig. 14), *Cercis siliquastrum, Crataegus azarolus* (Fig. 15), *Prunus ursina,* and others. The winter deciduous trees have a higher growth rate than have the evergreens, although the latter are physiologically active the whole year round; consequently, equal-sized trees of both types differ markedly from each other in age. The moisture requirements of the evergreens are considerably lower than those of deciduous trees, as is also evident from their water output through transpiration (see Chapter 8).

Fig. 11. *Arbutus andrachne.*

Fig. 12. *Quercus ithaburensis*

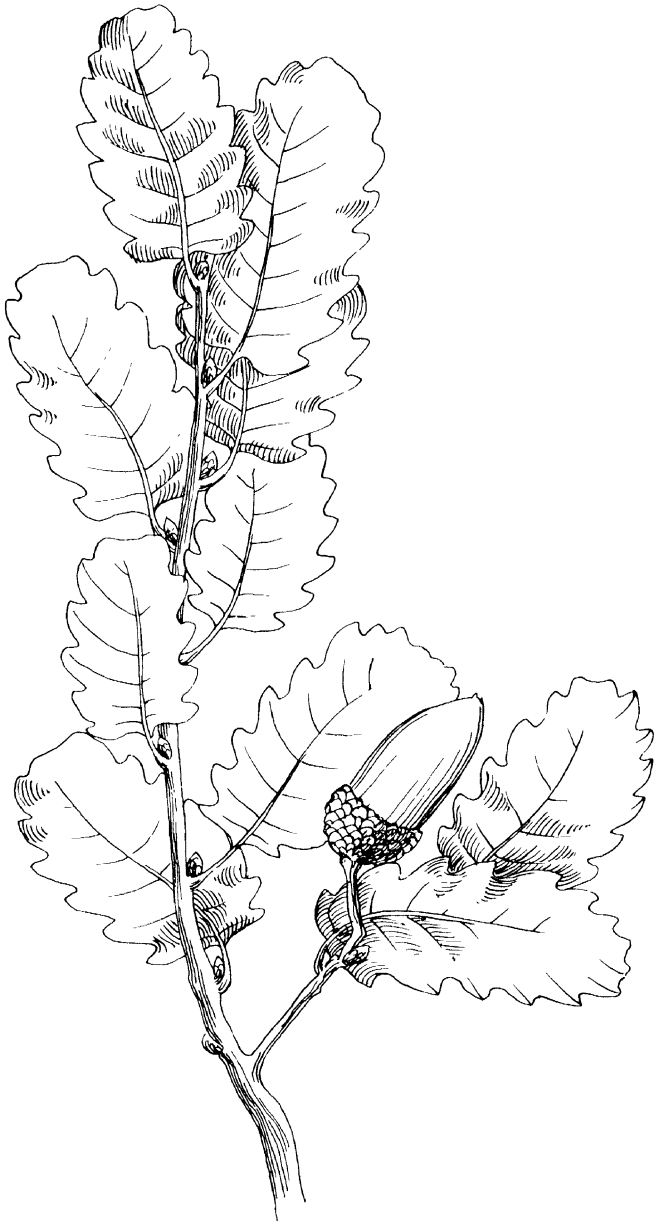


Fig. 13. *Quercus boissieri.*

Fig. 14. *Styrax officinalis.*

The local maquis and forests can be grouped in the following types: (1) pine forests (PINION HALEPENSIS alliance), (2) the deciduous tabor oak forests (QUERCION ITHABURENSIS alliance), (3) the evergreen oak maquis and forests (QUERCION CALLIPRINI alliance), and (4) the carob-lentisk maquis (CERATONIO-PISTACION alliance). Each of these types comprises a few associations, some of them commonly met with and others rare or fragmentary in occurrence.

1. ALEPPO PINE FOREST (PINION HALEPENSIS Alliance). This, the southernmost pine forest of the Mediterranean region, is domi-

Fig. 15. *Crataegus azarolus.*

nated by *Pinus halepensis* and is often accompanied by shrubs and trees of maquis and garigue, such as *Quercus calliprinos*, *Pistacia lentiscus*, *P. palaestina*, *Arbutus andrachne*, *Phillyrea media*, *Cistus villosus* and *C. salvifolius*, *Salvia triloba*, *Calycotome villosa*, and many other perennial and annual species, the occurrence and density of which depend on the amount of light available beneath the canopy

of the trees. It is confined to light-colored, highly calcareous rendzina soils derived from soft rocks of various Upper Cretaceous and Tertiary formations. The aleppo pine forest extends from sea level (in Lebanon) to 800 m. and more above sea level.

Remnants of this forest type scattered on rendzina soils all over the Mediterranean mountain range clearly indicate its former range of distribution. Larger stands have been preserved up to the present on Mount Carmel, in the mountains of southern Samaria, and in Gilead. The reasons for the extensive devastation of these forests are manifold. Pine forests are very susceptible to fire; unlike other forest and maquis trees, the aleppo pine is not able to renew growth from its stump and propagates from seed only. Also, the soft rendzina soils on which these forests grow are comparatively better fitted for hill farming than other mountain soils and their clearing was easy even for primitive man. Moreover, because of its most workable timber this pine has been largely exterminated.

The question whether the pine forest is a primary or secondary climax community may be considered here in some detail. As has already been mentioned, natural pine forests within the Mediterranean territory are exclusively confined to soft rendzina soils, while the evergreen oak maquis and forest, to be discussed later, occur both on rendzina and terra rossa. Pine seedlings are found abundantly on rendzina but never occur on terra rossa. The reason lies without doubt in the fact that on terra rossa soil moisture in exposed places is insufficient to support the pine seedling during the summer season, while on rendzina the available moisture content is considerably higher. Under a canopy of dense vegetation, where there is no moisture deficiency, pine seedlings fail to develop both on rendzina and terra rossa because of shade, which is detrimental to them. On the other hand, young specimens of the evergreen oak and other maquis trees are often found on rendzina, even in the shade of pine trees. When such underwood growth of the maquis remains untouched by man, it may develop into an oak forest and finally replace very short-lived pine trees which are unable to regenerate in the shade of this forest. The pine forest thus seems to represent a special sub-climax, the existence of which is conditioned by human interference with the broad-leaved underwood of this forest. In other words, while on terra rossa the successional sere, leading to the evergreen oak forest, advances directly from the garigue stage to the forest stage, pine forest may be intercalated between the last stages of the succession on light rendzinas. Where the underwood of such a forest is exposed to grazing or browsing the pine stage may last for a long period. The question as to whether pine forests form

a climax community within the evergreen oak forest area has also been raised in regard to western Anatolia by Schwarz (1936) and Walter (1956b). Presumably the circumstances there are similar to those prevailing in Palestine.

The following associations have been distinguished among the local pine forests:

a. Most common is the association of *Pinus halepensis–Hypericum serpyllifolium* (Eig, 1946). It is well represented in Mount Carmel (Fig. 16), where the following species were listed: *Pinus halepensis,*

Fig. 16. *Pinus halepensis–Hypericum serpyllifolium* association, rendzina soil, Mount Carmel.

Quercus calliprinos, Pistacia palaestina, P. lentiscus, Arbutus andrachne, Smilax aspera, Rubia olivieri, Genista sphacelata, Calycotome villosa, Cistus villosus, Hypericum serpyllifolium, Satureja thymbra, Cytisopsis dorycnifolia, Teucrium divaricatum, Fumana thymifolia, and many perennial and annual herbs.

b. The associations of *Pinus halepensis–Juniperus oxycedrus* and *Pinus halepensis–Cupressus sempervirens.* The former is found only in one locality in upper Galilee and the latter is very fragmentary in Gilead.

The successional stages of this forest have not been adequately studied. While it is certain that dwarf shrub communities dominated by *Poterium* and *Cistus* are often long-lived stages in the succession of this forest, it is also known that a pine forest can regenerate immediately on bare soft rendzina rocks.

Pinus halepensis is a tree obtaining a height of 10 m. or more and a maximum diameter of 50–60 cm. It is a comparatively short-lived species; specimens older than 160 years have not been found in Palestine. It has a rather shallow but much-branched root system and old trees in sites exposed to wind storms are occasionally uprooted. It flowers in early spring, with fertilization taking place about a year later; its cones ripen 15–17 months after flowering.

Pinus, like other conifers, is extremely economical in its water output. Its summer transpiration rate ranges from 75 mg. to 300 mg. water per 1 g. fresh weight per hour. In recent times *P. halepensis* has been successfully used for local large-scale afforestation on uncultivated land of the Mediterranean territory.

2. THE TABOR OAK FOREST (QUERCION ITHABURENSIS Alliance, Figs. 17, 18, 20). This type belongs to a large group of broad-leaved, deciduous forests, fairly common in some east Mediterranean countries, notably Turkey, Iraq, and Iran; some are known as *Vallonea* and *Aegilops* oak forests. Their acorns have a high tannin content and are therefore used commercially, especially in Turkey. In Palestine, this type of forest reaches its southern limit of distribution. Here three associations of this alliance have been distinguished.

a. The coastal tabor oak forest (QUERCETUM ITHABURENSIS ARENARIUM) is confined to the Sharon Plain, where only remnants of single stands or of scattered trees have been preserved to the present day. Their distribution indicates clearly that at one time that forest must have covered large extents of the sandy clay area between the rivers Yarkon and Zerka near Benyamina (Eig, 1933a). A grass community dominated by *Desmostachya bipinnata* accompanied this forest up to recent times and has lent to the landscape a savannah-like appearance. This grass community, of late largely destroyed by expanding citriculture, was in no way syngenetically related with the oak forest but conquered the area as soon as the latter was destroyed by man. This forest met its ultimate end in World War I, when trees were cut down by the Turkish army to provide locomotive fuel. Prior to that, as is evident from the accounts of travelers and other sources (Thomson, 1859; Volney, 1787; maps of the Palestine Exploration Fund, 1880, etc.), it was one of the largest and most beautiful oak forests of the region. From its remnants in Kefar Yona, Pardes Hanna, and other localities we can conclude that it was almost purely composed of oak without other arboreal associates. The numerous patches of batha and garigue vegetation scattered in the area allow the assumption that this forest has developed through a successional sere that included certain variants of POTERIETUM, CISTETUM, CALYCOTOMETUM, etc. Nothing, however, is known about the

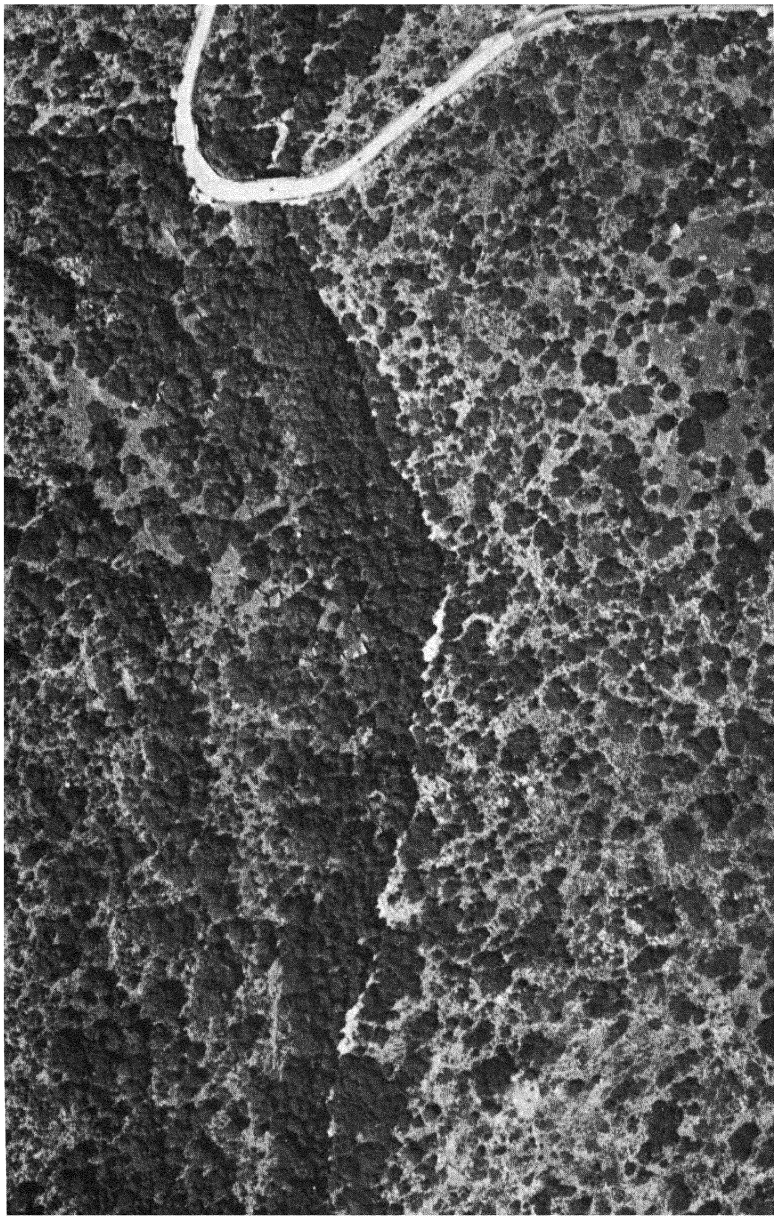


Fig. 17. *Quercus ithaburensis–Styrax officinalis* association, Alonim, lower Galilee (air view, Photogrammetric Institute, Jerusalem).

detailed progress of the sere. It is also not improbable that this deciduous, rather Sub-Mediterranean oak forest has formed a secondary climax in this area and has replaced a bygone evergreen maquis.

b. The typical tabor oak forest (association of *Quercus ithaburensis–Styrax officinalis*) is the most widespread community (Figs. 17, 18). Here the dominating tabor oak is accompanied by *Styrax officinalis* and under favorable ecologic conditions also by *Pistacia*

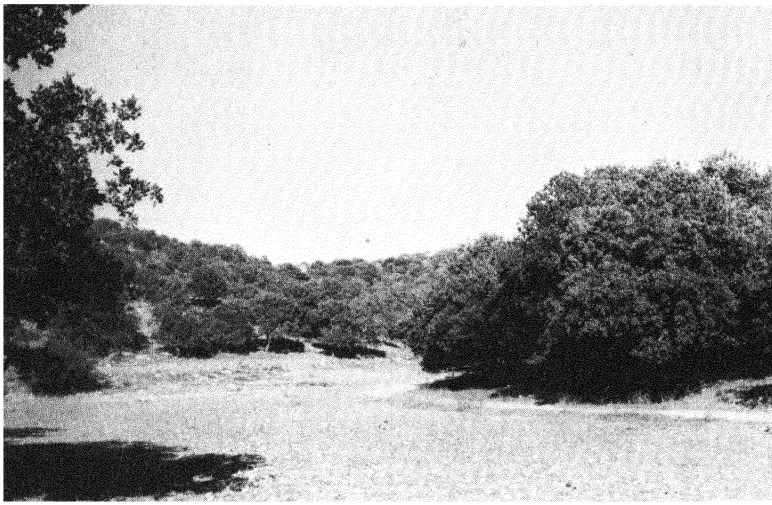


Fig. 18. *Quercus ithaburensis–Styrax officinalis* association, near Neve-Ya'ar, lower Galilee.

palaestina, *Crataegus azarolus*, *Cercis siliquastrum*, *Phillyrea media*, and others. This variant is well represented on the southwestern slopes of the lower Galilee and its remnants are also met with in the Ephraim Hills, Samaria. In a sample record taken in the environs of Alonim, lower Galilee, at a northern hillside, the following species have been listed: *Quercus ithaburensis*, *Q. calliprinos*, *Styrax officinalis*, *Crataegus azarolus*, *Phillyrea media*, *Pistacia palaestina*, *Calycotome villosa*, *Rhamnus palaestina*, *Clematis cirrhosa* (Fig. 19), *Smilax aspera*, *Rubia olivieri*, *Bryonia multiflora*, *Asparagus aphyllus*, *Tamus communis*, *Ruscus aculeatus*, *Anemone coronaria*, *Mandragora officinarum*, *Cyclamen persicum*, *Arum palaestinum*, *Thrincia tuberosa*, and many annuals. In this area the tabor oak forest is confined to dark rendzina soils derived from a Middle Eocene rock

Fig 19. *Clematis cirrhosa.*

with a fairly large percentage of organic matter in the topsoil; in some samples no lime was found. The dwarf shrub associations syngenetically connected with this climax forest are of a particular type, and a whole series of common batha and garigue subshrubs (e.g., *Cistus* spp., *Salvia triloba*, *Satureja thymbra*, and often also *Poterium*) do not participate in the seral stages leading to the climax. Eastwards this forest extends toward Mount Tabor and its surroundings, and single oak trees reach the eastern escarpments of the lower Galilee facing the Jordan Valley.

Fig. 20. Sacred forest of *Quercus ithaburensis* and *Pistacia atlantica*, near Dan, Huleh Plain.

c. The eastern tabor oak forest (association of *Quercus ithaburensis–Pistacia atlantica*) is chiefly limited to the western slopes of Gilead and Bashan, although remnants of it occur in the Huleh Plain. A sample record of this variant taken on a western slope of the Gilead Mountains opposite Gesher, at an altitude of 125 m., reads as follows: *Quercus ithaburensis*, *Pistacia atlantica*, *Crataegus azarolus*, *Amygdalus communis*, *Rhamnus palaestina*, *Styrax officinalis*, *Calycotome villosa*, *Ruta graveolens*, *Carlina corymbosa*, *Convolvulus dorycnium*, *Echinops viscosus*, *Ferula communis*, and many annual and perennial herbs. A beautiful remnant of this variant is preserved in the sacred wood known as "The Trees of the Ten" in the

Dan Valley north of Huleh (Fig. 20), where a group of over 100 aged and magnificent trees are associated with a few tall *Pistacia atlantica* specimens. No details are available on the succession of this marginal oak forest, which once occupied a large area of northeastern Palestine.

The tabor oak is less restricted in its edaphical requirements and does well in various soils (sandy clay, rendzina, basalt, and alluvial soils). It is, however, confined to lower altitudes only and never occurs in the mountains at altitudes above 500 m. It is not a very typical Mediterranean species, and its nearest relatives are found in interior Syria, Turkey, and Kurdistan. It is a shallow-rooting tree with broad deciduous leaves. It regenerates easily after having been cut down, and it is a fast grower and may attain a height of 20 m. Its moisture requirements are comparatively high and its hourly rate of summer transpiration ranges from 800 to 1000 mg. per 1 g. fresh weight. Its osmotic values are rather low. Taxonomically this species is exceedingly variable in the characters of its leaves and acorns. Some of its forms have erroneously been considered as species by Kotschy and others.

3. The Evergreen Oak Forest and Maquis (Quercion calliprini Alliance). This is the most typical and most common forest and maquis formation of the Mediterranean part of Palestine (and also of Syria, Lebanon, Turkey, and the Balkans). It has been subdivided into two units:

a. The *Quercus calliprinos–Pistacia palaestina* association (Eig, 1946) (Fig. 21). This occurs generally in the form of maquis and comprises, apart from the dominating *Quercus* and *Pistacia*, a series of other Mediterranean evergreen trees and shrubs such as *Laurus nobilis, Arbutus andrachne, Phillyrea media, Rhamnus alaternus, Viburnum tinus;* furthermore, the deciduous *Styrax officinalis, Cercis siliquastrum, Rhamnus palaestina, Crataegus azarolus,* and others. In addition, some undershrubs of the garigue and batha formations are often found. The most typical climbers of the maquis are *Clematis cirrhosa, C. flammula, Lonicera etrusca, Tamus communis, T. orientalis, Smilax aspera, Rubia olivieri, Bryonia syriaca,* and *Aristolochia altissima.*

This association occurs in a series of ecologic-floristic variants. One of them, in northern Galilee, under conditions of heavier rainfall and northern exposure, comprises in addition to the above-mentioned species *Quercus boissieri, Acer syriacum, Pyrus syriaca, Prunus ursina,* and *Sorbus trilobata.*

In view of ceaseless deforestation through hundreds and thousands of years it is astonishing to encounter today large expanses of dense

and well-preserved maquis. This is no doubt due to the ability of its trees and shrubs to withstand human interference by being able to regenerate from their underground stems. The average height of this maquis does not exceed 4 m., but its coverage sometimes reaches 100 per cent and penetration into it may become impossible.

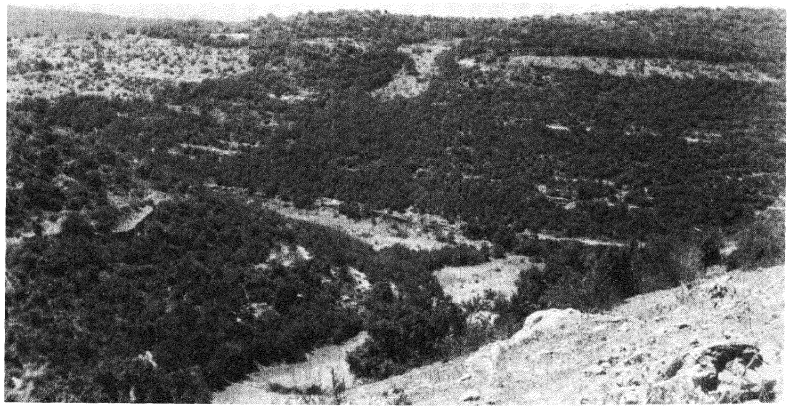


Fig. 21. *Quercus calliprinos–Pistacia palaestina* association, between Meiron and Sa'asa (Upper Galilee).

The maquis affords shelter to a great many beautiful bulb and tuber plants such as *Lilium candidum* (Fig. 22), *Paeonia corallina*, *Allium dumetorum*, *Fritillaria libanotica*, *Hyacinthus orientalis*, many species of *Tulipa*, *Allium*, *Colchicum*, *Crocus*, *Orchis*, *Ophrys*, some shade-demanding ferns, and others. Where the maquis is less dense, it offers optimal growth conditions for a wealth of annual and perennial herbs.

This type of maquis is common throughout the western mountain belt from the foot of the Lebanon up to the Judean Mountains in the south. As it approaches its southern boundary it gradually loses many of its components, but the two leading species remain within the association up to its terminal limits of distribution.

Large areas of former maquis have been devastated severely and turned into dwarf shrub vegetation dominated by *Poterium*, *Cistus*, and other batha and garigue plant communities. At present these communities are in a progressive phase of succession toward the maquis-forest climax community. In the climax area of the *Quercus-Pistacia* association, the earlier stages of successional development have been observed on abandoned fields in the vicinity of Jerusalem.

During the first two years after abandonment of the fields, annual

segetals disappear while certain perennial weeds such as *Ononis leiosperma* and *Linum mucronatum* persist. This weed residue becomes associated or replaced by certain perennial grasses, such as *Dactylis glomerata, Phalaris bulbosa, Hordeum bulbosum,* and *Oryzopsis holciformis,* as well as by some hemicryptophytic dicots, such as

Fig. 22. *Lilium candidum* in the maquis on rocky slopes of Wadi Fallah, Mount Carmel.

Polygonum equisetiforme, Carlina corymbosa, and *Echinops viscosus.* The next stage is marked by the relatively rapid invasion of the most common batha and garigue elements. *Poterium spinosum* (Fig. 23) or *Thymus capitatus* (Fig. 24), depending on the soil character, are the first on the scene They are often accompanied at a later stage by *Cistus salvifolius, C. villosus, Thymbra spicata, Calycotome villosa,* etc. These associations occupy the terrain for some time. Maquis trees, in spite of being abundantly available in the vicinity for seed supply, do not succeed in entering the open field occupied by the batha and garigue shrubs. Their seeds germinate only close to and under the canopy of the trees.

Ten years of observation did not enable us to follow up further stages in development towards the local climax, but from evidence collected elsewhere it is quite obvious that batha and garigue communities prepare the ground for the successful germination and establishment of high shrubs and trees of the maquis by promoting

humus formation and increasing the soil moisture content. An exact estimate as to the time required to enable the establishment of the maquis cannot be made, but it is evident that soon after an oak or another maquis tree has entered a batha or garigue community it

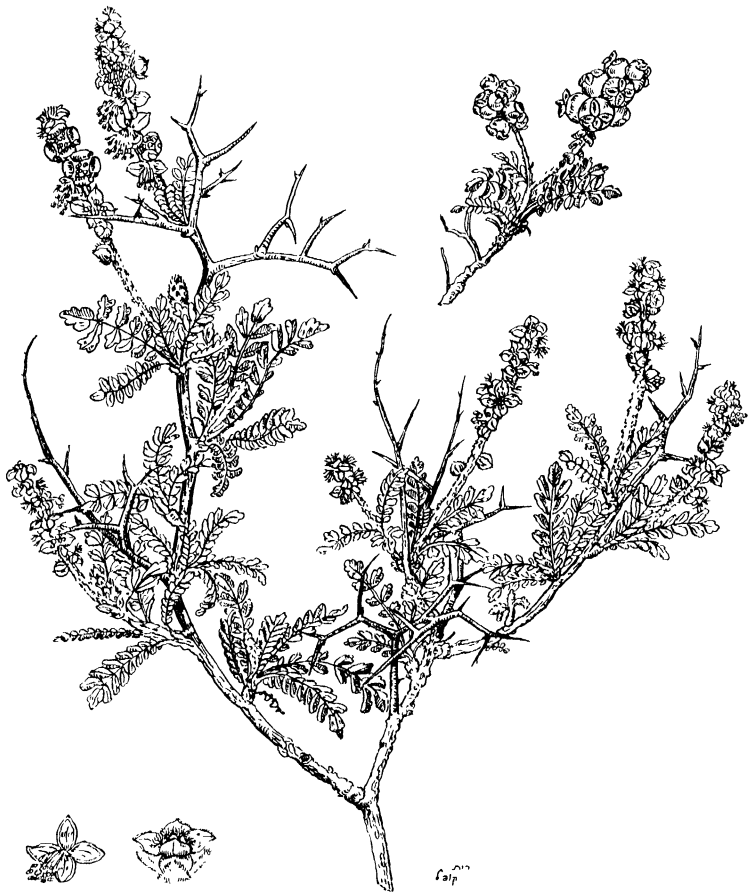


Fig. 23. *Poterium spinosum.*

outgrows and overshades the neighboring light-demanding dwarf shrubs and eventually kills them. The course of succession and the length of time each stage may dominate the area varies with the microclimate, the degree of soil maturity, and possibly with other factors. In all cases, however, it is obvious that within the entire

area of the *Quercus-Pistacia* climax the POTERIETUM SPINOSI is one of the most important seral communities of the succession.

The *Quercus-Pistacia* community demands relatively low winter temperatures and as a rule does not occur in the mountains below

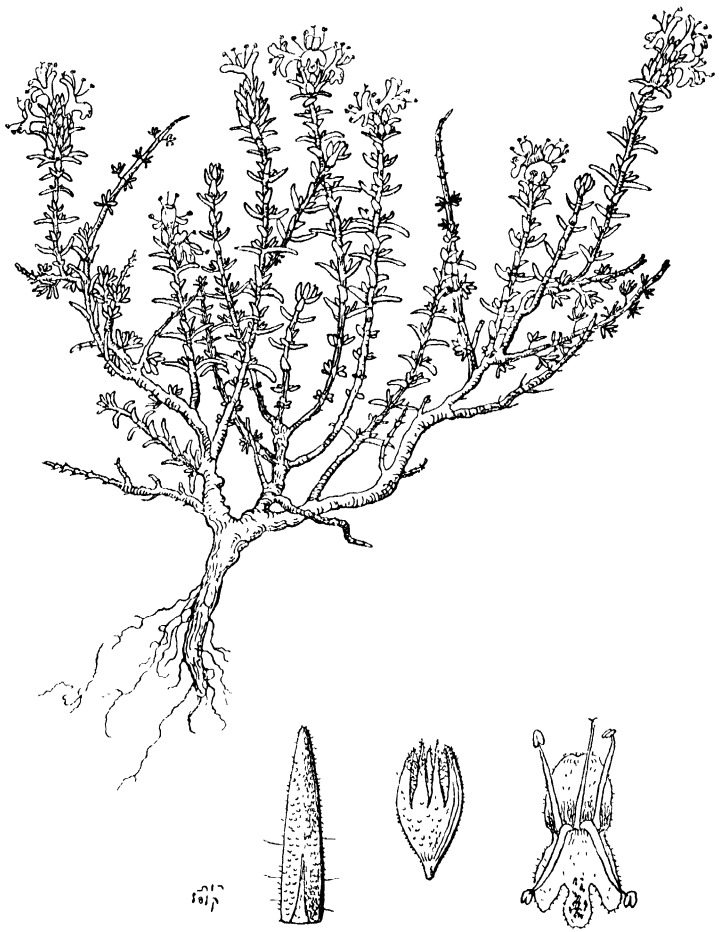


Fig. 24. *Thymus capitatus.*

an altitude of 200 m. It is most characteristic of Mediterranean terra rossa but also occurs on certain variants of rendzina. As to the soil moisture, it has been found that in certain areas the upper layers dry out during summer to the wilting point and below, so that the

annuals die out, and only deep-rooting perennials and arboreal plants that can utilize the moisture of deeper soil layers persist. The water intake of shrubs and trees is thus entirely dependent upon the dimensions and depth of their roots. Regarding the water turnover, two types of species can be distinguished in the maquis: those with a low and those with a high transpiration rate. To the first group belong the olive tree, carob tree, *Laurus nobilis, Pistacia lentiscus,* and *Arbutus andrachne,* with an hourly summer transpiration rate not exceeding 500 mg. per 1 g. fresh weight. To the second group belong *Quercus calliprinos, Crataegus azarolus, Amygdalus communis, Pistacia palaestina,* and *Rhamnus palaestina,* with an hourly transpiration rate between 500 and 1000 mg. or more per 1 g. fresh weight.

Quercus calliprinos is an East Mediterranean vicariad of the West Mediterranean *Q. coccifera.* It is a species of bewildering variability which deserves an intensive genetic and taxonomic study.

b. The *Quercus calliprinos–Juniperus phoenicea* association. This is encountered in the southwestern part of Transjordan (Edom) at an altitude of between 1000 and 1700 m. This forest occupies a strip of about 50 km. in length and has its southernmost limit in the neighborhood of Petra. Apart from *Quercus calliprinos* and *Juniperus phoenicea* it also comprises *Crataegus azarolus, Pistacia palaestina, P. atlantica, Rhamnus palaestina,* as well as *Daphne linearifolia,* which does not occur elsewhere in Palestine. The underwood of this loose forest is occupied by steppe or desert shrubs. According to Kasapligil (1956), the association as such is rather limited here in space, and there are two variants: one in which *Juniperus phoenicea* forms pure stands or is associated with *Pistacia atlantica,* and the other in which *Quercus calliprinos* is the almost single tree constituent of the forest. The former is confined to Nubian sandstone, the latter to calcareous soil.

4. The Carob-Lentisk Maquis (Ceratonio-Pistacion Alliance, Figs. 26, 27). In its outer appearance this type of maquis is reminiscent of a savannah forest. On a rather dense carpet of low shrubs, consisting of *Pistacia lentiscus* and other associates, occur scattered carob trees which often attain a height of 4 m. or more. Both of the leading plants are evergreen.

The carob-lentisk maquis occupies large stretches in Israel but is almost entirely lacking in Transjordan. It is widespread on the western foothills of the mountain belt, and also occurs on the eastern slopes of Galilee and Samaria. Besides, it occupies consolidated dunes and kurkar hills in the Sharon Plain north of Natanya. It

does not ascend the mountains to altitudes above 300 m., except in some eastern escarpments of the Samaria Mountains. Although many of its components may also occur higher in the mountains, the community as such is strikingly thermophilous. In accordance with its ecologic relations and its floristic composition it should be subdivided into three associations:

a. The typical carob-lentisk association (CERATONIETO–PISTACIETUM LENTISCI TYPICUM). This is confined to the western foothills along the mountain belt of Israel. Typical stands are found in the Matsuba-Eilon area (Galilee), on Mount Carmel, including the kurkar hills of the Atlith area, in the Hartuv-Beit Guvrin area, and further south to the latitude of Hebron. The soil varies from terra rossa to rendzina and kurkar sandstone. While this community has been well preserved in certain parts of the area, it has been almost tracelessly destroyed in the central part of foothills between Hulda and Tul-Karem.

In this association the carob trees and *Pistacia* shrubs are accompanied by numerous Mediterranean chamaephytes, such as *Cistus villosus, C. salvifolius, Calycotome villosa, Salvia triloba, Ruta graveolens, Poterium spinosum, Thymbra spicata, Phlomis viscosa* (Fig. 25), and many others. The main climbers are *Asparagus aphyllus, Rubia olivieri, Clematis cirrhosa,* and *Smilax aspera.* Of the perennial grasses *Hyparrhenia hirta, Andropogon distachyus, Phalaris bulbosa,* and *Dactylis glomerata* may be mentioned.

This association can be subdivided into two variants, a northern one which comprises Mediterranean shrubs and also *Olea europaea* var. *oleaster,* and a southern variant in which *Olea* is often lacking and in which some of the Mediterranean shrubs are replaced by semisteppe ones as well as by *Hyparrhenia hirta* stands. The northern variant resembles West Mediterranean OLEETO-LENTISCETUM (Braun-Blanquet *et al.,* 1952).

b. The sand dune carob-lentisk association (CERATONIETO–PISTACIETUM LENTISCI ARENARIUM, Figs. 26, 27). This type occurs on consolidated sand dunes, notably in the northern part of the Sharon Plain, while fragments of it are also found in the surroundings of Nahariya (north of Acre). Here the two leading species, *Ceratonia* and *Pistacia,* are accompanied by a series of shrubs, such as *Lycium europaeum, Ephedra alte, Ballota philistaea, Retama raetam* var. *sarcocarpa, Artemisia monosperma* (Fig. 28), and *Asparagus stipularis.* In more advanced stages, *Prasium majus, Ruta graveolens, Cistus villosus, Clematis cirrhosa, Rhamnus palaestina,* and even *R. alaternus* may enter the association. The area between Natanya and Caesarea is the only part of the coastal sand dune belt

Fig. 25. *Phlomis viscosa.*

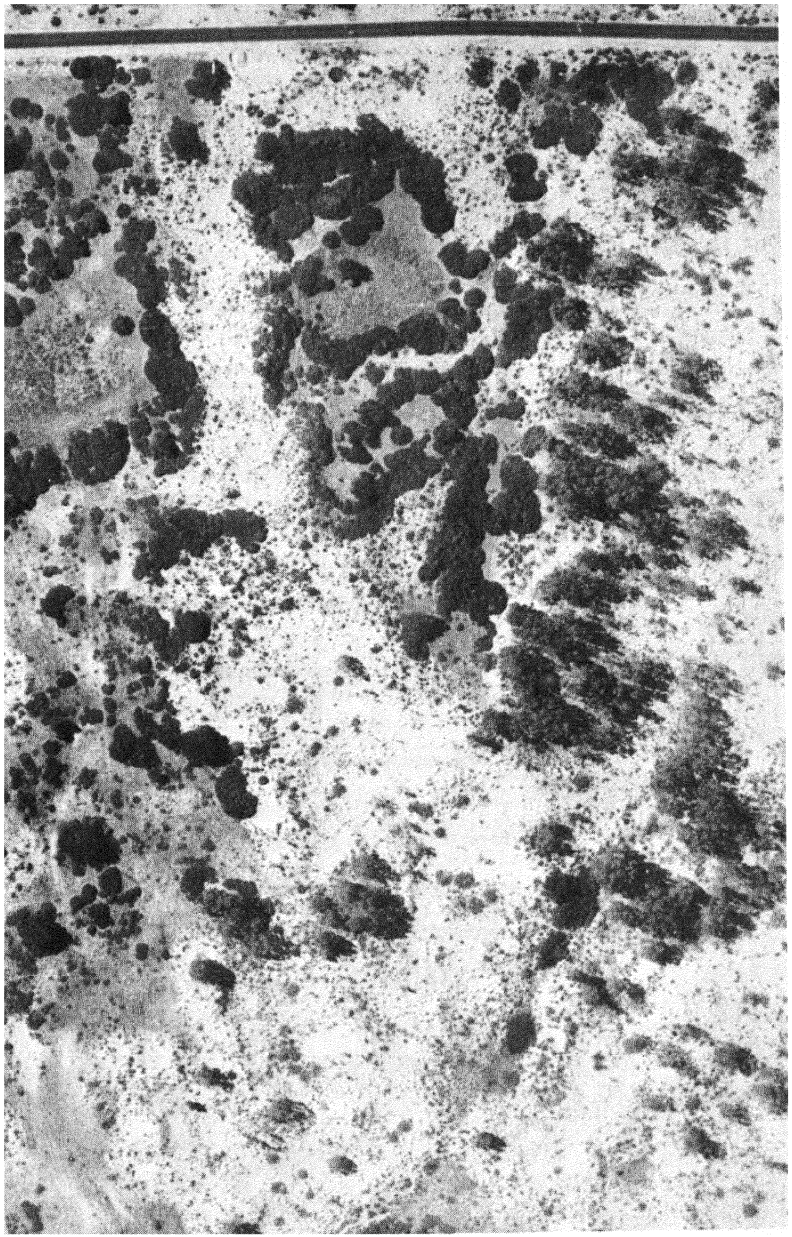


Fig. 26. *Ceratonieto–Pistacietum lentisci*, sands, Caesarea, Sharon Plain. (Air view, Photogrammetric Institute, Jerusalem).

where this association is well developed, due to the action of some very efficient sand-binding shrubs, such as *Artemisia monosperma*, *Retama raetam* var. *sarcocarpa*, and *Polygonum palaestinum*. Some successional stages from initial stages of sand dune vegetation up to the stages of the climax can be observed here. On the other hand, unusual windstorms blowing from the sea may destroy the established climax community and bring about the start of a new cycle of seral development.

Fig. 27. *Ceratonieto–Pistacietum lentisci*, on wind-swept dunes near Caesarea, Sharon Plain.

c. The eastern carob-lentisk association (CERATONIETO–PISTACIETUM LENTISCI ORIENTALE). This association is located on the eastern escarpments of the lower Galilee and Samaria exposed to Irano-Turanian influence. Accordingly, it comprises, in addition to the *Ceratonia* and *Pistacia lentiscus* and some Mediterranean dwarf shrubs, some plants of semisteppe and Irano-Turanian communities, such as *Ballota undulata*, *Ononis natrix*, *Zizyphus lotus* (Fig. 29), *Pistacia atlantica*, *Amygdalus communis*, and *Phlomis brachyodon*.

A variant of the latter association is found on the eastern slopes of the upper Galilee opposite the Huleh Plain. *Pistacia lentiscus* is almost entirely lacking here and is replaced by *Styrax officinalis* and *Amygdalus communis*.

All the above associations of *Ceratonia-Pistacia* form climaxes in their respective areas. Some of these associations or their variants also occur in other East Mediterranean countries and can be regarded

Fig. 28. *Artemisia monosperma.*

Fig 29. *Zizyphus lotus.*

as vicariads of West Mediterranean OLEETO-LENTISCETUM (Braun-Blanquet *et al.*, 1952). The main tree of these communities is the economically most important *Ceratonia siliqua,* a dioecious evergreen tree with pods that are valuable as forage. In many places where natural vegetation has been erased completely, the wild carob tree escaped destruction and was often grafted with cultivated varieties. At present, wider-scale plantations of carob trees for forage are taking place in the foothill region of Israel.

The wild carob tree is economical in its water consumption and has an hourly transpiration rate of only 300–500 mg. water per 1 g. fresh weight. Like most of the maquis trees, it has long horizontal and superficial roots side by side with strong vertical ones reaching a depth of several meters and penetrating rock fissures as well as soft solid rocks. Of phenological interest is the fact that it is the only tree of the Mediterranean maquis which flowers mainly in autumn and produces its fruits about ten months later, in late summer. *Pistacia lentiscus* is an evergreen dioecious shrub reaching about 1 m. in height; very rarely, it assumes the habit of a small tree. Its roots reach a considerable depth and are able to penetrate solid but not too hard rocks.

* * *

In the eastern and southern borderland of the Mediterranean territory of Palestine are very poor fragments of a steppe maquis represented by almond trees and hawthorn shrubs. The interspaces between the widely scattered shrubs or trees of *Amygdalus communis* and *Crataegus azarolus* are often covered with semisteppe dwarf shrub plants. This kind of a "steppe-maquis" at one time supposedly formed an easily recognizable belt which fringed the woody Mediterranean vegetation on its steppe and desert boundary. It is probably an extremely impoverished variant of maquis which has lost its true Mediterranean elements in its approach toward the steppe.

Another type of a borderland wood community is the *Pistacia atlantica* steppe-forest of which well-developed stands are still preserved in eastern Transjordan and in some mountain ranges of the Syrian Desert, the Negev, and the eastern fringe of the maquis zone. Since its recent distribution suggests that it belongs to the Irano-Turanian region, it will be dealt with in the following chapter.

In concluding this discussion on Mediterranean maquis and forests, some remarks may be added concerning their latitudinal sequence and zonal arrangement. As they expand southward, the maquis lose many of their components. So, for instance, *Juniperus oxycedrus, Sorbus trilobata, Prunus ursina,* and *Acer syriacum* reach

their southern terminus in the upper Galilee. Mount Carmel is the southernmost area for *Laurus nobilis, Genista sphacelata, Pistacia saportae, Olea europaea* var. *oleaster,* and *Viburnum tinus. Quercus boissieri, Cercis siliquastrum, Spartium junceum,* and *Rhamnus alaternus* reach their southern limit in the central Judean Mountains, while *Pinus halepensis, Quercus calliprinos, Crataegus azarolus, Ceratonia siliqua, Pistacia lentiscus, Styrax officinalis,* and others extend southward up to the confines of the maquis zone south of Hebron or nearly so. There is also a similar decrease in components in the westerly to easterly direction, although the regularity of this gradual diminution is interrupted by the Jordan Valley. Anyhow, the Transjordan maquis are rather poor in Mediterranean trees.

The peculiar zonation of the Mediterranean and borderland maquis and forest, which is the result of exposure and distance from the sea, as well as altitude, is illustrated in the following cross section from the western coast via the western mountains to the Jordan Valley (Huleh Plain) in the east. The *Ceratonia–Pistacia* maquis are encountered in the coastal plain and in the western foothills. The next altitudinal belt is occupied by the *Quercus calliprinos–Pistacia palaestina* maquis, which in higher elevations also includes fragments of the mesophytic deciduous forest dominated by *Quercus boissieri.* On the eastern slope of the mountains there is another belt of *Ceratonia–Pistacia* maquis and then throughout the Huleh Plain there are stands and remnants of the *Quercus ithaburensis* forest and also small groups and scattered trees of *Pistacia atlantica.* The latter also penetrated deeply into the drastically deforested areas of the carob and *Quercus ithaburensis* climax zones. In a parallel west-to-east cross section at the latitude of Jerusalem there appear remnants of the *Ceratonia–Pistacia* maquis in the west and *Quercus calliprinos–Pistacia* maquis at higher points up to Jerusalem, while within that city and further east of it single trees of *Pistacia atlantica, Crataegus azarolus,* and *Amygdalus communis* mark the close of the Mediterranean woodland here. The absence of corresponding *Ceratonia–Pistacia* and *Quercus ithaburensis* belts east of Jerusalem is explained by the high altitude of the eastern mountain side here. A glance at the vegetation map (Map 5) reveals this more or less symmetrical arrangement of the Cisjordan Mediterranean woodland. The intercalation of the *Quercus ithaburensis* forest in the northern Sharon Plain between the *Ceratonia* maquis belt of the coastal plain and that of the foothills may be regarded as the result of a secondary shifting of climaxes (see Chapter 4).

Garigue and Batha Vegetation (POTERIETALIA SPINOSI and BALLOTETALIA UNDULATAE Orders). "Garigue" is a French term for sclero-

phyllous scrub that consists generally of chamaephytes and nanophanerophytes 1 m. or so in height. In Palestine and elsewhere in the Mediterranean region, several plant communities belong to this formation. The leading plants in these communities here are *Calycotome villosa*, *Satureja thymbra*, *Cistus villosus*, *C. salvifolius*, *Phlomis viscosa*, and *Salvia triloba*. The term "batha" is a Biblical word applied by Eig (1927) to Mediterranean dwarf shrub associations not exceeding a height of 50 cm. and consisting of dwarf shrubs and perennial herbs. Leading plants of the local batha are *Poterium spinosum*, *Thymus capitatus*, *Fumana arabica*, *F. thymifolia*, *Teucrium polium*, *T. divaricatum*, *Hyparrhenia hirta*, *Salvia graveolens*, *Ballota undulata*, and many others. The two above formations are not always well differentiated from each other.

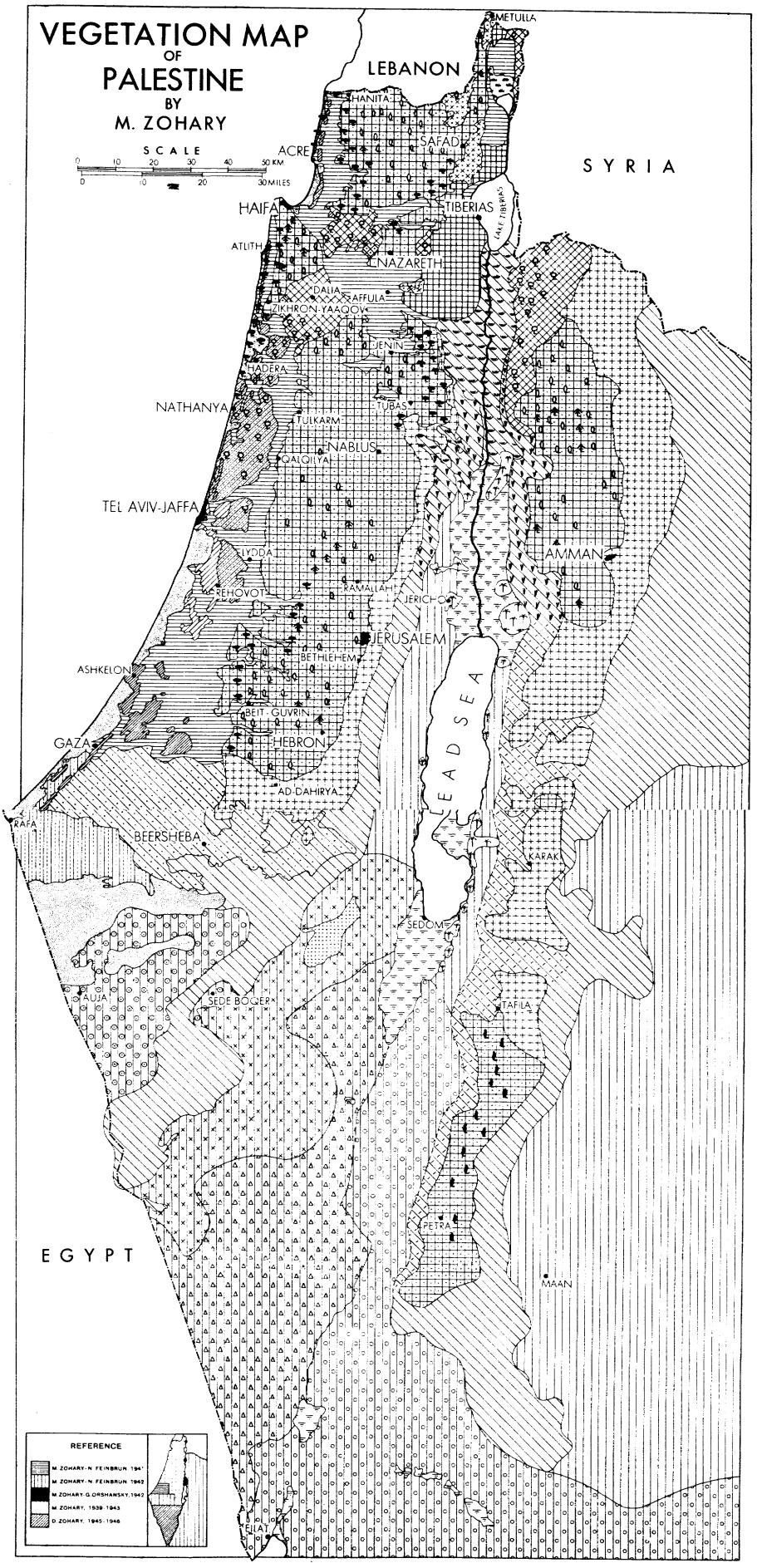
At present, garigue and batha dominate the uncultivated Mediterranean mountain and hill country. They are so expressive of the landscape that unexperienced observers find it hard to look upon them as only temporary stages in the succession toward arboreal climax vegetation. Only on the eastern and southern borders of the Mediterranean territory do garigue and batha communities occasionally form ultimate vegetation stages. Amid the Mediterranean territory it is not always easy to decide whether the batha and garigue communities are in a stage of progressive development toward woodland or whether they are in a stage of retrogression toward complete bareness. Generally, batha communities precede those of garigue in the successional sere; at other times the two are syngenetically independent of each other.

The number of plant communities of the batha and garigue is considerable. Some of them are well distinguished from each other, others only by their dominant and codominant species. According to their distribution and to their floristic make-up, the bathas and garigues of Palestine have been divided into two orders: POTERIETALIA and BALLOTETALIA. The former comprises mostly chamaephytic plant communities of the Mediterranean territory, and the latter mostly hemicryptophytic bathas of the Mediterranean–Irano-Turanian borderland, and accordingly also includes steppe plants.

The following is a list of the main batha and garigue associations:

POTERIETALIA SPINOSI ORDER

1. CALYCOTOMION VILLOSAE alliance
   a. CALYCOTOMETUM VILLOSAE TYPICUM
   b. CALYCOTOMETUM VILLOSAE LITTORALE
   c. CALYCOTOMETUM VILLOSAE SEMISTEPPOSUM



Map 5. See following pages for legend.

LEGEND FOR MAP 5: VEGETATION OF PALESTINE

1. Climax district of evergreen maquis and forests, destroyed and reoccupied by typical Mediterranean batha and garigue vegetation, e g., POTERIETUM SPINOSI, THYMETUM CAPITATI, CALYCOTOMETUM VILLOSAE, CISTETUM SALVIFOLII Segetal vegetation consists of the *Carthamus tenuis–Ononis leiosperma* assoc.

2. As above, with remnants of evergreen maquis and forests of the *Quercus calliprinos–Pistacia palaestina* assoc

3. As above, with remnants of evergreen maquis of the CERATONIO–PISTACION LENTISCI alliance

4. As above, with remnants of *Pinus halepensis–Hypericum serpyllifolium* forest assoc.

5. Climax district of the oak-juniper association (*Quercus calliprinos–Juniperus phoenicea*) in southern Transjordan

6. Climax district of the tabor oak forest destroyed and reoccupied by hemicryptophytic batha. Segetal vegetation as in No. 1

7. As above, with remnants of the tabor oak–storax forest (*Quercus ithaburensis–Styrax officinalis* assoc.)

8. Mosaics of forest and maquis remnants of types 2 and 7

9. Hemicryptophytic Mediterranean batha in eastern Galilee. Supposed climax–forests and maquis of *Quercus ithaburensis* at lower altitudes and *Q calliprinos* and *Q boissieri* at higher ones

10. As above, with remnants of maquis and forests of the above oak species

11. District of Mediterranean semisteppe batha communities, e g., ONONIDETUM NATRICIS, *Salvia dominica–Ballota undulata* assoc., *Echinops viscosus–Carlina corymbosa* assoc., sometimes accompanied by scattered trees of deciduous steppe forests (e g, *Amygdalus communis, Crataegus azarolus* in the west and south, or *Pistacia atlantica* in eastern Gilead).

12. Sandy clay vegetation of the coastal plain mainly *Desmostachya* (*Eragrostis*) *bipinnata–Centaurea procurrens* assoc. Most of its components also participate in the segetal vegetation of the district.

13. As above, with remnants of tabor oak forest.

14. Mediterranean batha and garigue on kurkar hills of the coastal plain mainly littoral variants of POTERIETUM SPINOSI, THYMETUM CAPITATI, CALYCOTOMETUM VILLOSAE, CISTETUM (in the northern part) Comprises also HELIANTHEMETUM ELLIPTICI (in the southern part).

15. As above, with remnants of the CERATONIETO–PISTACIETUM LENTISCI TYPICUM.

16. Mosaics of types 12 and 14.

17. Alluvial plains: climax vegetation destroyed and mostly unknown. In some parts remnants of subtropical *Hyparrhenia* savannah. Segetal vegetation consists mainly of the PROSOPIDION FARCTAE alliance. Hydrophilous vegetation occurring in these plains is not marked on the map.

18. Mediterranean hemicryptophytic semisteppe bathas associated with *Zizyphus lotus* Climax vegetation–supposedly forest of *Quercus ithaburensis–Pistacia atlantica* assoc. (in the northern part of the district).

19. Climax district of Irano-Turanian shrub steppes, mainly of the ZIZYPHION LOTI alliance.

20 Climax district of Irano-Turanian shrub steppes, mainly of the RETAMETALIA RAETAM order.

21. Climax district of Irano-Turanian dwarf shrub steppes, mainly of the ARTEMISIETALIA HERBAE-ALBAE order.

22. Irano-Turanian steppes on loess soil, primary vegetation almost entirely destroyed. Segetal vegetation mainly ACHILLEETUM SANTOLINAE.

23 Irano-Turanian dwarf shrub steppes on western escarpments of Transjordan. Vegetation not adequately known, probably consisting of the ARTEMISIETALIA HERBAE-ALBAE order

24. Steppes of *Artemisia monosperma* and annual grasses on sandy-loess soils of western Negev.

25. Saharo-Sindian hammada deserts of Transjordan, consisting mainly of the following alliances. ANABASIDION ARTICULATAE, ZYGOPHYLLION DUMOSI, CHENOLEION ARABICAE, SUAEDION ASPHALTICAE

26 Mosaics of ZYGOPHYLLION DUMOSI on hillside hammadas and of HALOXYLION ARTICULATI on loess plains.

27. Saharo-Sindian hammada deserts of central Negev, consisting mainly of the ZYGOPHYLLION DUMOSI alliance

28 Barren hammada deserts of central and southwestern Negev. Vegetation mainly in depressions and wadi beds, consisting of the ANABASIDION ARTICULATAE alliance and the ACACIETUM TORTILIS assoc

29 Sand and sandy hammada deserts in Arava Valley and Edom, dominated by the HALOXYLETUM SALICORNICI and the HALOXYLETUM PERSICI.

30 Salines of Arava Valley, lower Jordan Valley, and Edom, partly sterile and partly inhabited by the *Arthrocnemum glaucum–Tamarix tetragyna* assoc., SUAEDETUM PALAESTINAE, ATRIPLICETUM HALIMI, SALSOLETUM TETRANDRAE, NITRARIETUM RETUSAE, etc. Vegetation of coastal salines not marked on map.

31. Mobile and semimobile sand dune vegetation of the coastal plain and coastal Negev, consisting mainly of the ARTEMISION MONOSPERMAE and the LOTION CRETICI alliances.

32. As above, with the CERATONIETO–PISTACIETUM LENTISCI ARENARIUM in the north

33 Sand dune vegetation of interior Negev, mainly of the ANABASIDION ARTICULATAE alliance.

34. Enclaves of tropical vegetation, mainly *Zizyphus spina-christi–Balanites aegyptiaca* assoc. and ACACIETUM TORTILIS.

35 Hydrophilous vegetation of Hulch swamps, mainly of the PHRAGMITION alliance Other areas of hydrophilous vegetation not marked on map.

2. CISTION VILLOSI alliance
   a. CISTETUM VILLOSI TYPICUM
   b. CISTETUM VILLOSI LITTORALE
   c. SALVIETUM TRILOBAE
   d. SATUREJETUM THYMBRAE
   e. PHLOMIDETUM VISCOSAE
3. POTERION SPINOSI alliance
   a. POTERIETUM SPINOSI TYPICUM
   b. *Poterium spinosum–Thymelaea hirsuta* assoc.
   c. POTERIETUM SPINOSI SEMISTEPPOSUM
4. THYMION CAPITATI alliance
   a. THYMETUM CAPITATI TYPICUM
   b. *Thymus capitatus–Hyparrhenia hirta* assoc.
   c. THYMETUM CAPITATI SEMISTEPPOSUM
   d. FUMANETUM THYMIFOLIAE

BALLOTETALIA UNDULATAE ORDER

1. BALLOTION UNDULATAE alliance
   a. *Salvia dominica–Ballota undulata* assoc.
   b. ONONIDETUM NATRICIS
   c. ECHINOPETUM BLANCHEANI
2. FERULION COMMUNIS alliance
   a. FERULETUM COMMUNIS
3. ECHINOPO–CARLINION alliance
   a. *Echinops viscosus–Carlina corymbosa* assoc.
   b. *Convolvulus dorycnium–Carlina corymbosa* assoc.
   c. *Psoralea bituminosa–Echinops viscosus* assoc.
   d. ASPHODELETUM MICROCARPI

A few of the associations listed above will be dealt with in further detail.

Of the garigue associations a sample record of the SALVIETUM TRILOBAE, taken at the western slope of Mount Carmel, is given here: *Salvia triloba, Calycotome villosa, Rhamnus palaestina, Poterium spinosum, Pistacia lentiscus, Teucrium divaricatum, Fumana thymifolia, Rubia olivieri, Asparagus aphyllus, Smilax aspera, Thrincia tuberosa, Ranunculus asiaticus, Cyclamen persicum, Anemone coronaria, Salvia hierosolymitana, Arisarum vulgare,* and many annuals. The presence of *Pistacia* and *Rhamnus* indicates that this association is here advancing toward the local climax, which is CERATONIETO-PISTACIETUM.

Another example of a garigue is the CISTETUM VILLOSI TYPICUM, of which the following plants (and many others) have been listed near Kiryath Anavim, west of Jerusalem: *Cistus villosus, C. salvi-*

folius, Phlomis viscosa, Poterium spinosum, Teucrium polium, T. divaricatum, Stachys cretica, Phagnalon rupestre, Scorzonera pappposa, Lactuca cretica, Helichrysum sanguineum, Majorana syriaca (Fig. 30), *Serratula cerinthifolia, Bellis silvestris, Thrincia tuberosa, Salvia judaica, Oryzopsis holciformis, Smilax aspera,* and *Rubia olivieri.*

Of the batha vegetation one of the most common alliances is that dominated by *Poterium spinosum* (POTERION SPINOSI). A sample record of a POTERIETUM SPINOSI TYPICUM, taken on a northern slope of the Judean Mountains near Jerusalem, includes the following species; *Poterium spinosum, Cistus villosus, Fumana thymifolia, F. arabica, Calycotome villosa, Teucrium polium, T. divaricatum, Hyparrhenia hirta, Andropogon distachyus, Dactylis glomerata, Osyris alba, Helichrysum sanguineum, Rhamnus palaestina, Phlomis viscosa, Micromeria nervosa, Eryngium creticum, Salvia judaica, Rubia olivieri, Orchis anatolicus, Ophrys fusca, Ranunculus asiaticus, Thrincia tuberosa, Bellis silvestris, Medicago orbicularis, Onobrychis squarrosa, Trifolium campestre, T. stellatum, T. purpureum, Lotus peregrinus, Lathyrus aphaca, Aegilops peregrina, Bromus scoparius,* and others.

A marginal association is the POTERIETUM SPINOSI SEMISTEPPOSUM, which occurs in eastern and southern border regions of the Mediterranean territory. It comprises, in addition to typical Mediterranean associates, a number of species of the semisteppe batha associations and several Irano-Turanian species, e.g., *Echinops blancheanus, Erysimum crassipes, Carlina involucrata, Noëa mucronata, Linaria aegyptiaca, Scrophularia xanthoglossa, Artemisia herba-alba* (Fig. 31), *Anchusa strigosa,* and others.

On the light soils of the coastal plain the *Poterium spinosum–Thymelaea hirsuta* association (Fig. 32) is characterized by the presence of a number of psammophytes accompanying the dominant *Poterium spinosum.*

A sample record of the *Thymus capitatus–Hyparrhenia hirta* association, taken on a kurkar hill in the central Sharon Plain, comprises the following species: *Thymus capitatus, Hyparrhenia hirta, Teucrium polium, Fumana thymifolia, F. arabica, Asphodelus microcarpus, Thymelaea hirsuta* (Fig. 33), *Helianthemum ellipticum, Alkanna tinctoria, Leopoldia maritima, Tulipa sharonensis, Plantago albicans, P. cretica, Astragalus callichrous, Medicago littoralis, Anthemis leucanthemifolia, Erodium telavivense, Lotus villosus,* and many others.

This triple vicariism of batha communities in mountainous, semisteppe, and coastal zones also characterizes certain garigue alliances,

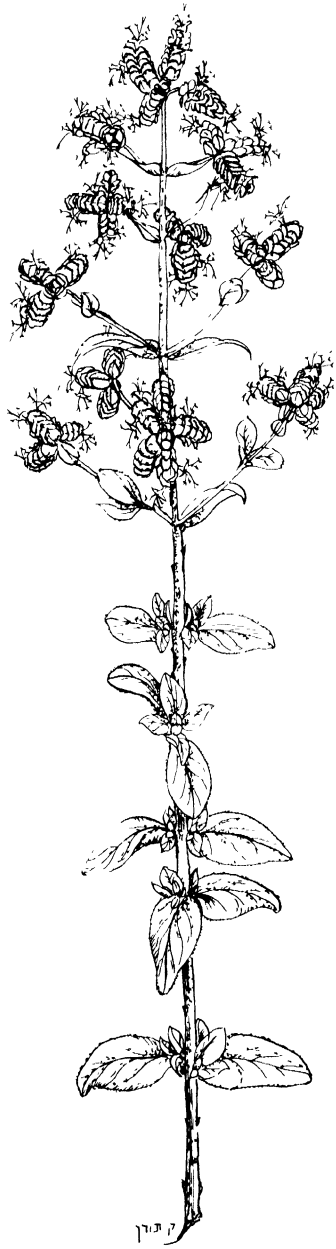


Fig. 30. *Majorana syriaca.*

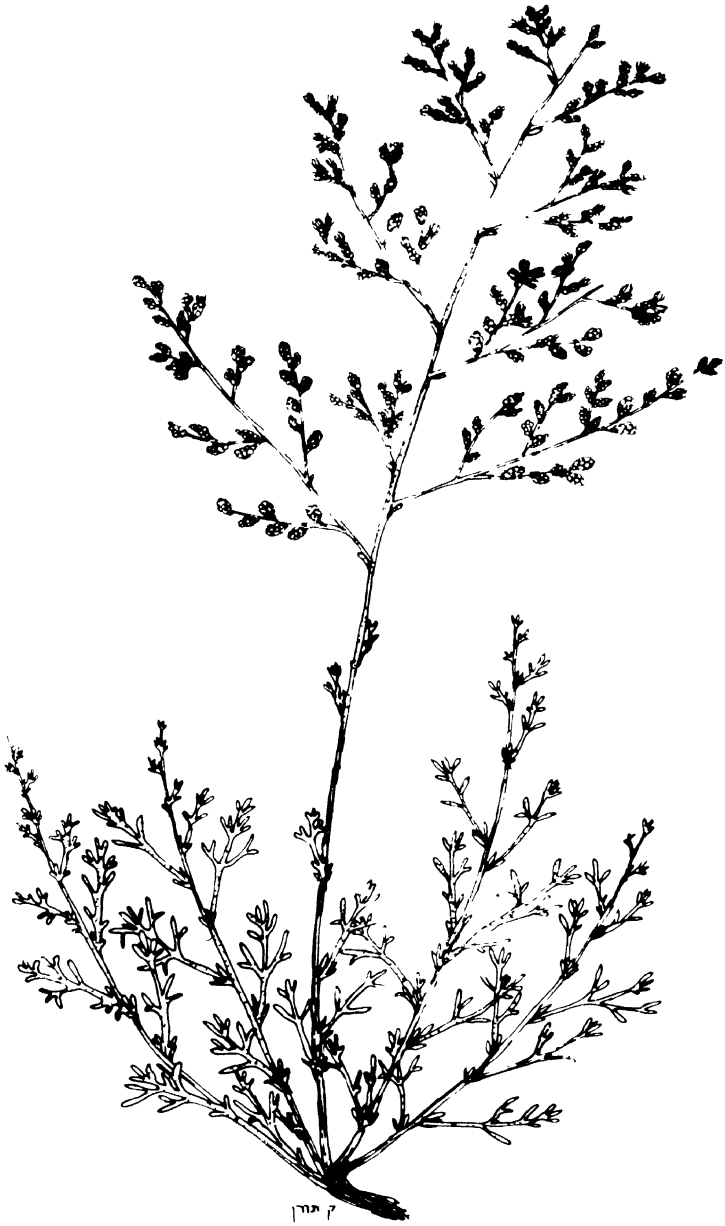


Fig. 31. *Artemisia herba-alba.*

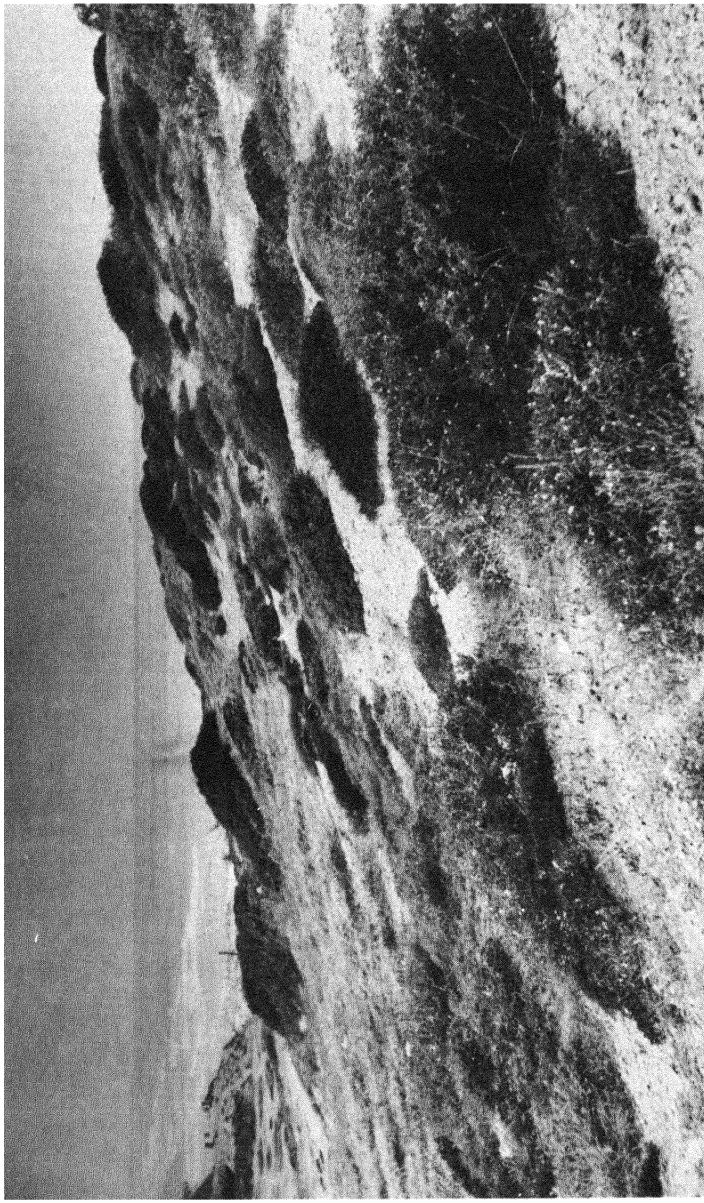


Fig. 32. *Poterium spinosum–Thymelaea hirsuta* association, on kurkar sandstone of the Mediterranean coast near Herzliya, Sharon Plain.

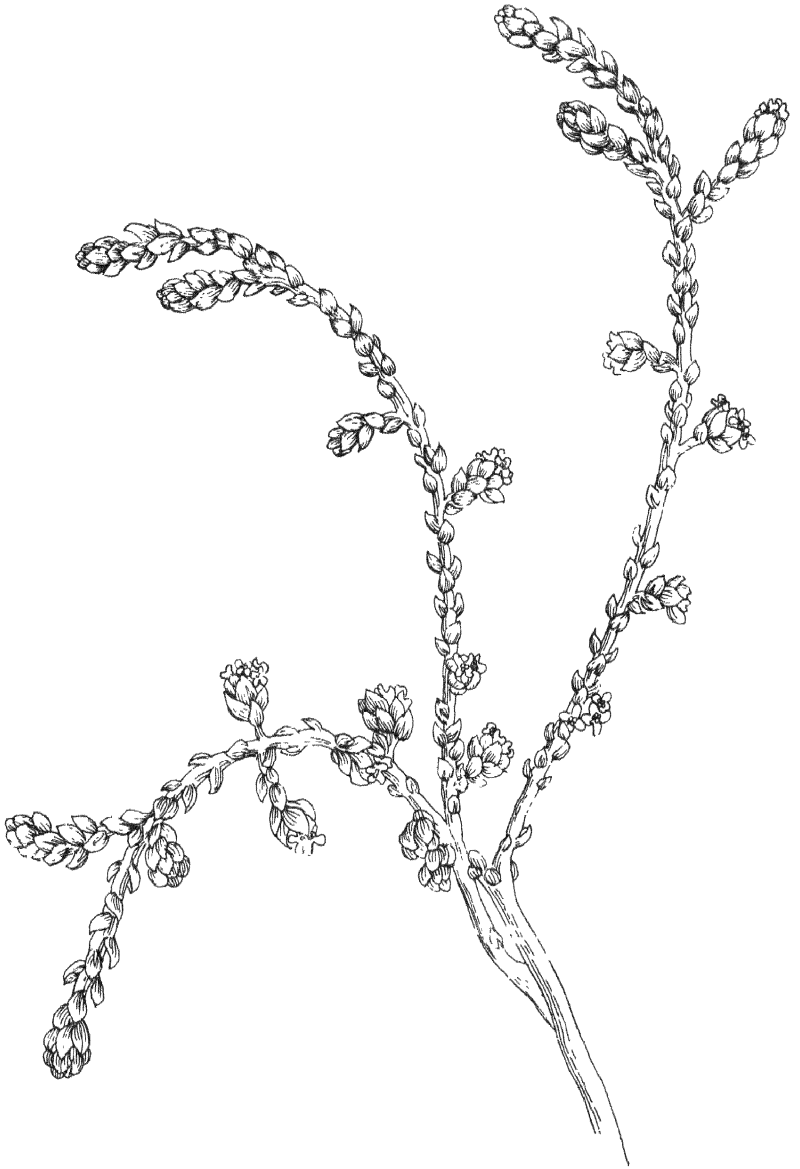


Fig. 33. *Thymelaea hirsuta.*

as also the alliances of CERATONIO-PISTACION and QUERCION ITHABURENSIS.

Among the batha associations of the Mediterranean–Irano-Turanian borderland that are included in the BALLOTETALIA order, the *Salvia dominica–Ballota undulata* association is most common on soft chalky rocks and on white-grayish soil. The following species of this association have been listed on a hill near Shoval, northwest of Beersheba: *Salvia dominica, Ballota undulata, Astragalus feinbruniae, Eremostachys laciniata, Noëa mucronata* (Fig. 34), *Phlomis brachyodon, Cachrys goniocarpa, Heliotropium rotundifolium, Lycium europaeum, Asphodelus microcarpus, Hyparrhenia hirta, Anchusa strigosa, Alkanna strigosa, Gypsophila rokejeka,* etc. This type of semisteppe batha is not seral but probably forms the vegetation climax of the area. Part of its constituents are Irano-Turanian species.

In addition to chamaephytes and nano-phanerophytes, garigue and batha formations contain an abundance of winter annuals and geophytes belonging to the genera *Anemone, Ranunculus, Colchicum, Tulipa, Allium, Bellevalia, Scilla, Crocus, Iris, Orchis, Ophrys,* etc. These and scores of species of the families Cruciferae, Leguminosae, Compositae, Labiatae, Umbelliferae, and others adorn the spring landscape with a variegated carpet of flowers but disappear as summer drought sets in.

Most of the dominating plants in the batha and garigue formations are xeromorphous, light-demanding, and economical in their water output. One of their most efficient means of reducing transpiration during the dry season is the replacement of the comparatively large winter leaves by small leaflets, mostly arranged in bud-like brachyblasts. In summer the surface of the transpiring body may become reduced to as little as half its area in the winter season. The hourly intensity of summer transpiration calculated per 1 g. of fresh weight ranges from 160 to 800 mg., according to species. Different species of the same habitat behave differently in their water turnover.

Batha and garigue are the last safeguards against soil erosion in the mountain slopes. When, as is often the case, this vegetation is used as source of fuel and is carelessly eradicated, heavy soil erosion results in a rapid wearing away of the shallow soil layer from the mountain sides. In the course of time vast stretches in the very center of the Mediterranean territory have so been denuded that many Arab agricultural settlements have been abandoned. In such "man-made deserts" the arboreal vegetation does not re-establish itself for long periods.

Fig. 34. *Noëa mucronata.*

The rate at which new soil formation can take place depends on the nature of the bedrock. Centuries of weathering are required for soil restoration from hard limestone and dolomitic rock, while bare soft chalks and marly limestone may support vegetation also in an intact state, first by crustaceous lichens and then by vascular lithophytes. The lithophytes themselves participate in the process of weathering by disintegrating the rocks and hereby accelerating soil formation.

Mediterranean Vegetation on Rocky and Stony Ground

(Varthemietea iphionoidis Class)

Within this class of vegetation, plant communities are included which are confined to stony habitats such as rocks, rock crevices, stone fences, walls, cave entrances, and rubble heaps. These habitats have only one feature in common, namely, the stony substratum; otherwise, they differ from one another in many ways and their respective vegetation units are quite distinct. In accordance with such a diversity of sites and vegetation units the class has been divided into three orders, each comprising several alliances. It should, however, be remarked that the classification of this type of vegetation is only tentative and more comprehensive treatment of this subject in the future may alter our view of it considerably.

The Order Varthemietalia. As has already been mentioned, there are considerable areas within the Mediterranean territory which, as a result of abuse of vegetation through generations, have become denuded to their rock. Where these rocks are not too hard, they are sparsely inhabited by a number of associations grouped within the alliance of VARTHEMION. Some of these lithophytes are of supreme importance in soil formation because their roots can penetrate deeply into solid rocks, which crack as the roots thicken. The two most important plant communities of this habitat are VARTHEMIETUM IPHIONOIDIS and STACHYDETUM PALAESTINAE.

VARTHEMIETUM IPHIONOIDIS (Fig. 35) is confined either to bare solid and comparatively hard rocks or to the amorphous "nari" layer, which forms a fairly thick crust on various rock formations. The association comprises several chamaephytes which are able to germinate in minute pits of the rock surface, and which then send their roots into the unbroken limestone rock. The most important components of this very loose association are *Varthemia iphionoides* (Fig. 36), *Podonosma syriaca,* and *Ballota rugosa. Varthemia* is a light-demanding composite and occupies the "roof" of projecting rocks, while the two other species mentioned do not resent shade and grow

mostly on the "walls" of the rock. Accompanying those true lithophytes are a number of plants which grow in small crevices or hollows where small amounts of soil have accumulated

STACHYDETUM PALAESTINAE, another association very similar to the former and not well differentiated from it, is confined to the more northern latitudes of Palestine. The dominant *Stachys palaestina* and *Micromeria serpyllifolia* have the same ability to penetrate more or less intact limestone with their roots.

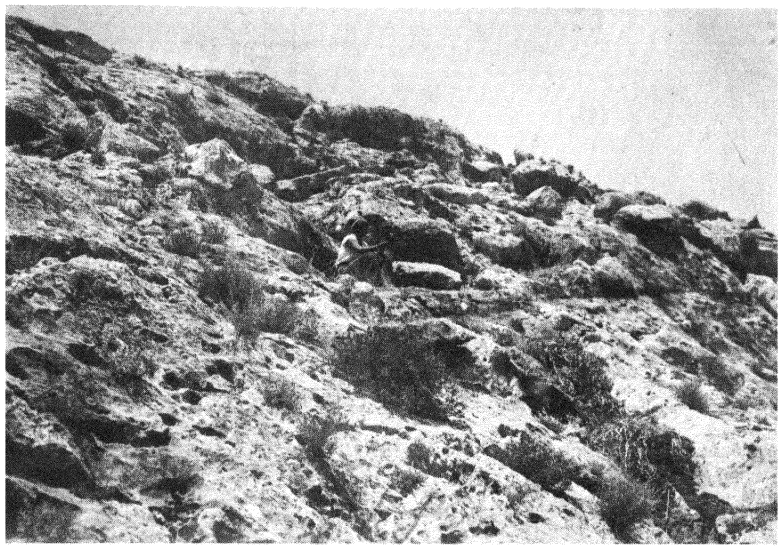


Fig. 35. *Varthemietum iphionoidis*, near Et-Taiyibe, Judean Desert.

Other lithophytic communities of the VARTHEMION occur in northern Palestine. Their dominant species are *Pennisetum asperifolium*, *Michauxia campanuloides*, *Centaurea speciosa*, and *Dianthus pendulus*. Detailed knowledge of these communities is inadequate so far.

The ecology of some lithophytes was studied by M. Zohary and Orshan (1951), who found that the roots of *Varthemia*, *Stachys*, *Podonosma*, and *Ballota* are able to penetrate comparatively hard rocks. The flattened and poorly branched roots were followed up within the rock to depth of 50 cm. Attempts to germinate the seeds of the above plants on the naked rock have failed, but seedlings which started to enter the rock have been found in nature. These seeds germinate in very small pits or cavities of the rock, in which some dust has accumulated. As the rootlet grows in length, it twists

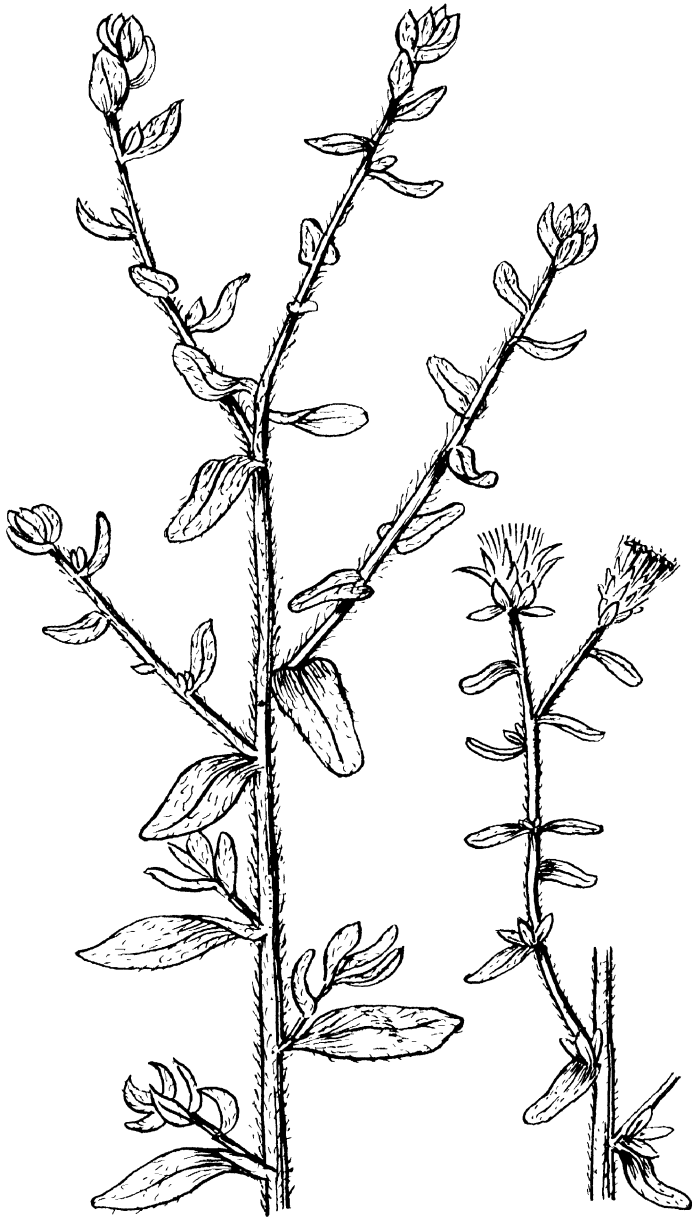


Fig. 36. *Varthemia iphionoides.*

spirally and then descends inside the rock. The pit, ranging from between 0.5–1.5 cm. both in depth and in diameter, is sooner or later filled up with the thickening root crown which staples the whole pit, so as to exclude percolation of rain water entirely. Thus it is the root itself which, by exuding acids, forces its way into the rock. Since *Varthemia* and *Podonosma* are active the whole year round and their water output through transpiration is rather high, the question arose as to how these plants manage to obtain their water from the "dry" rock. Measurements in this line have shown that the field capacity of such rocks is comparatively high, ranging from 8 per cent to 22.4 per cent when referred to dry matter. From calculation of the plant coverage and the mobility of water in the rock it was concluded that sufficient moisture is available in these rocks to balance the ratio of intake and output of moisture by the plants.

To the UMBILICION alliance of this order belongs the association of *Umbilicus intermedius–Allium subhirsutum*. This is confined to old stone fences with small soil pouches between the layers of stones or in the crevices. Apart from *Umbilicus* and *Allium* the following are found here: *Erophila minima, Crepis hierosolymitana, Veronica cymbalaria, Cyclamen persicum, Parietaria judaica, Taraxacum cyprium*, several species of mosses and liverworts of the genera *Targionia, Lunularia, Barbula, Tortula, Grimmia, Encalypta, Camptothecium*, and others.

A number of communities of the PARIETARION alliance are confined to old walls in towns and cities. Their leading species are *Parietaria judaica, Hyoscyamus aureus, Antirrhinum siculum, Capparis spinosa* var. *aegyptia*, etc. Their occurrence near human dwellings suggests a ruderal character. In all cases the mortar into which their roots penetrate contains some amounts of refuse. Moist walls and cave entries are often inhabited by *Adiantum capillus-veneris* and certain mosses.

On the rubble heaps of field margins a particular plant community predominated by *Cynocrambe prostrata* takes a foothold. Other associates here are *Galium articulatum, Cicer pinnatifidum, Veronica cymbalaria, Vicia sericocarpa, Crepis bulbosa, Vicia angustifolia* f. *amphicarpa, Pisum fulvum* var. *amphicarpum*, etc. Most of these plants have very long hypo- or epicotyls which enable their seeds to germinate among the stones at a considerable depth from the surface of the heap.

6

Steppe and Desert Vegetation

The Concepts of Steppe and Desert

Though the terms "steppe" and "desert" have been used widely in botanical literature, no precise definition has so far been given to those concepts. Regel (1939), Gradmann (1934), Rikli (1913), Walther (1912), Del Villar (1925), Emberger (1930, 1931, 1933), and many others have discussed the steppe-desert concepts at length or have attempted to differentiate between the two. However, their various definitions have no common basis, not even when they are backed by climatic formulas.

Very generally, a steppe is understood to comprise a timberless landscape with an open but a more or less continuous vegetation of xerophilous shrubs, semishrubs, and herbs. Even under arid conditions the annual amount of rainfall allows, at the least, sporadic dry farming in steppe areas. Deserts may under certain conditions grow the same type of vegetation but with a lower and intermittent coverage. Their limited rainfall excludes any possibility of farming except in oases or flooded lowlands. Use is also made of the terms "semisteppe," "semidesert," and "desert-steppe," the definitions of which are so vague that they can hardly be applied in classification of vegetation zones.

To omit confusion, the following amendment to the above definitions is suggested: steppes are areas lacking arboreal vegetation as a result of climatic factors, possibly precipitation; yet they display a more or less continuous vegetal cover composed of life forms other than trees. As to deserts distinction should be made between three types: (1) "rain deserts," i.e., areas in which vegetation is patchy and very sparse but still maintained by rainfall; (2) "runoff deserts," i.e., areas in which the amount of precipitation is insufficient to support any kind of vegetation except in depressions and low-lying places in

which, in addition to the small amount of rainfall, ground water or runoff moisture accumulates; and (3) absolute deserts in which there is altogether no sign of vegetation.

These types are well defined and can be used in land classification within the Near Eastern deserts and elsewhere. The Irano-Turanian territory of Palestine, as delimited in Chapter 3, consists mainly of steppes and "rain deserts" whereas the Saharo-Sindian territory comprises "rain deserts," "runoff deserts," and absolute deserts. It should, however, be remarked that from the ecologic point of view plants growing in temporary waterways, depressions, and runnels within a desert surrounding can hardly be regarded as desert plants, since such sites obtain a considerable amount of runoff moisture in addition to rainfall. Plants growing here may differ largely in their ecologic behavior, or at least in their water relations, from other plants which subsist on the small amount of rainfall alone. This latter type of plant living under sublethal conditions displays the characteristics generally attributed to desert plants. Strictly speaking, and paradoxical though it may sound, there are no true desert plants in "runoff deserts." The reason that students of moisture ecology have arrived at controversial conclusions as to the water ecology of desert plants lies in the fact that topography, as a major ecologic factor in deserts, was not always taken into account. The desert-plant ecologist ought to select his research material from true xeric habitats, where plants are exposed to a minimum of atmospheric moisture, and not from depressions and beds of temporary streams. The ecology of desert plants will be referred to again in greater detail in Chapter 8.

Nature of Plant Communities in Steppes and Deserts

For the sake of brevity, the term "desert vegetation" is here applied in a wider sense to comprise the vegetation of both the Irano-Turanian and the Saharo-Sindian territory of Palestine. The relatively large number of plant communities found in deserts is surprising in view of the extreme environmental conditions and the relative poverty of species. However, close examination of the various habitats often reveals that slight ecologic variations are sufficient to promote the occurrence of clearly different communities. This is because under desert conditions, plants, especially perennials, are much more susceptible to minor differences of the environment than are plants that grow under more humid conditions. The amount of annual rainfall, ranging as it does from 350 mm. to 25 mm., is in itself a supreme factor in dividing the desert into a number of life zones and habitats. Next to moisture, topography is the

most important factor. Slight surface elevations or depressions will promote the development of certain plants and hinder that of others. Furthermore, exposure, degree of salinity, soil structure and texture, as well as temperature and relative humidity strengthen the diversification of habitats and vegetation.

The plant communities of deserts differ in many of their characters from those of humid zones. Plant sociology could hardly have evolved from a study of desert vegetation, where the plant communities are unstable in composition. In fact, the number of components of a community varies from year to year with the amount of annual rainfall, and in extremely dry years the annual components of the community may be lacking altogether. After consecutive years of drought even perennials may fail to develop. In 1933, for example, *Poa sinaica*, which dominates large stretches of the Syrian Desert, did not produce any aerial shoots. This and other desert species of *Poa* are highly plastic in their growth behavior. In altogether rainless years the bulbils fail to sprout and in years of limited rainfall only the basal leaves may appear, while flowering culms develop in rainy years only. With certain other hemicryptophytes and chamaephytes, also, the production of aerial parts depends on the amount of annual rainfall, so that in dry years leaves may fail to develop.

The annual components of desert communities are not only unstable in their presence, as such, but also exhibit as a rule a very wide ecologic range. Hence, their adherence to definite plant communities is rather feeble. They may occur in various plant communities if they find sufficient moisture to complete their life cycle. Thus these "desert wides" can hardly characterize particular plant associations, in contrast to the perennials, notably the chamaephytes, which are the only permanent representatives of a community.

The very feeble plant coverage is one of the most characteristic features of desert vegetation. Some areas have as little as 5 per cent of their surface covered by plants. Over large stretches of hammada the percentage is considerably lower than that; here an observer is sometimes unable to take in two plants with the same glance. Hence the terms "association" or "community" can hardly be applied to such a scattered population.

The Expansion Drive of Desert Plants

It is a well-known fact that there is a steady ebbing of plants from marginal to less marginal habitats wherever the native vegetation is affected by man. Mediterranean districts that border upon desert are gorged with desert immigrants, "waiting" everywhere for man-made vacua in non-desert habitats. With the rehabilitation of the

primary vegetation, these aliens are pushed back to their previous habitats. However, where man is in control of the habitat, desert plants may assume a permanent foothold within more humid areas.

The migration pressure of desert plants in a north and westward direction makes itself felt in the coastal light soil belt and especially in the dunes. Here scores of annual and perennial desert plants are associated with typical Mediterranean elements in permanent plant communities. Among desert plants that have advanced along the coastal plain are *Retama raetam, Artemisia monosperma, Polygonum palaestinum, Neurada procumbens, Citrullus colocynthis, Atractylis flava, Panicum turgidum,* and *Helianthemum ellipticum.*

Other penetration areas of desert plants are the large alluvial plains of the Mediterranean territory that have been cultivated since ancient times. There is, for example, the Irano-Turanian *Prosopis farcta* that has become a predominant plant of the segetal habitats here. A similar example is *Desmostachya bipinnata.* Among the series of true Irano-Turanian plants which played a considerable part among the segetals are *Cephalaria syriaca, Bongardia chrysogonum, Leontice leontopetalum, Allium schuberti, Astragalus oocephalus, Gladiolus atroviolaceus,* and *Gundelia tournefortii.*

The Vegetation of the Irano-Turanian Territory

The predominant habitats of this territory are non-saline gray calcareous steppe soil, loess soil, and rocky hills, with an annual rainfall of 350–200 mm. Vegetation consists of steppe forest, thorny and broomlike brushwoods, and dwarf shrub communities (Eig, 1946). They are included within a single class, the ARTEMISIETEA HERBAE-ALBAE, which comprises the following units:

ZIZYPHO-PISTACIETALIA ORDER

1. PISTACION ATLANTICAE alliance
   a. PISTACIETUM ATLANTICAE
2. ZIZYPHION LOTI alliance
   a. ZIZYPHETUM LOTI
   b. *Zizyphus lotus–Retama raetam* assoc.
   c. *Zizyphus lotus–Zizyphus spina-christi* assoc.

RETAMETALIA RAETAM ORDER

1. RETAMO-PHLOMION alliance
   a. PHLOMIDETUM BRACHYODONTIS
   b. *Phlomis brachyodon–Blepharis edulis* assoc.
   c. RETAMETO–RHUDETUM TRIPARTITAE
   d. RETAMETO–PERIPLOCETUM

ARTEMISIETALIA HERBAE-ALBAE ORDER

1. ARTEMISION HERBAE-ALBAE alliance
   a. ARTEMISIETUM HERBAE-ALBAE–ONONIDETOSUM
   b. *Artemisia herba-alba–Asphodelus microcarpus* assoc.
   c. ARTEMISIETUM HERBAE-ALBAE TYPICUM
   d. NOËETUM MUCRONATAE
2. HALOXYLION ARTICULATI alliance
   a. HALOXYLETUM ARTICULATI
   b. *Anabasis haussknechtii–Poa sinaica* assoc.
   c. ANABASIDETUM HAUSSKNECHTII SUBSEGETALE

Only few of the above associations will be dealt with below.

The PISTACIETUM ATLANTICAE association, a type of steppe forest in which *Pistacia atlantica* is the dominant or only tree, occurs in the mountains of the Negev, in eastern Gilead, on the eastern branches of the Anti-Lebanon mountain range and on some mountain ridges of the northern Syrian Desert. The stands, no doubt remnants of different plant associations, are too fragmentary and have not been sufficiently studied. They are composed of widely scattered trees with a comparatively close cover of Irano-Turanian dwarf shrubs in the interspaces.

Small stands or single aged trees of *Pistacia* also occur on the eastern slopes of the Galilee Mountains, on the eastern slopes of the Samarian and Judean Mountains, and also in the steppes east of Amman as well as in Edom. The relic nature of this forest type is evidenced by the fact that nowhere have seedlings of this tree or young trees been found.

P. atlantica, the "eila" of the Bible (or the species mainly referred to by that name), is a handsome deciduous tree which may attain a considerable age and sometimes grows to a height of 20 m. Its small drupes are edible, especially when roasted. It is one of the fast-growing native trees and has been widely used as a stock for *Pistacia vera,* especially in eastern Syria and in North Africa.

The ZIZYPHETUM LOTI (Fig. 37) is a brushwood association in which *Zizyphus lotus* is the dominant species. While its original range of distribution in Palestine is on the hillsides facing the central Jordan Valley between Wadi Far'a and Beit Shean, its occurrences further north on the hillsides that face the upper Jordan Valley and elsewhere are secondary and are the outcome of an intrusion of *Zizyphus* into deforested lands on the edge of the Mediterranean territory. A sample record of the ZIZYPHETUM taken near Wadi Malik, south of Beit Shean, shows the following composition:

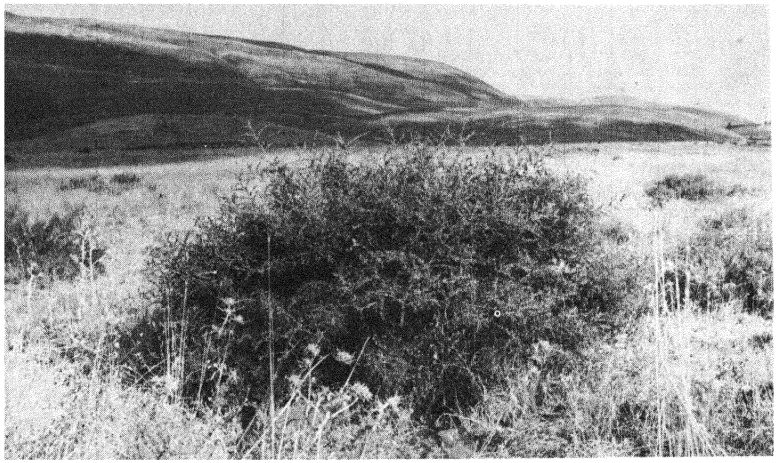


Fig. 37. *Zizyphetum loti*, basalt soil, near Hagoshrim, upper Galilee.

Zizyphus lotus
Ballota undulata
Salvia graveolens
Echinops blancheanus
Carlina corymbosa
Asphodelus microcarpus
Ferula communis
Alkanna strigosa
Astragalus macrocarpus
Gypsophila rokejeka
Anchusa strigosa
Salvia horminum
Scabiosa prolifera
Ajuga chia
Lycium europaeum
Majorana syriaca
Onosma fruticosa
Pterocephalus involucratus
Elymus geniculatus

There are also many others

Zizyphus lotus (see Fig. 29) is an intricately branched shrub of the Rhamnaceae family, 1–2 m. high. It has simple, deciduous leaves with thorny stipules and small edible drupes. Its general range of distribution extends from Spain through western North Africa to Syria. In North Africa it is often associated with *Pistacia atlantica*. There is a considerable gap in the continuity of its distribution between Cyrenaica and the Jordan Valley. In Palestine *Z. lotus* is a thermophilous species limited to altitudes not exceeding 300 m. above sea level. Small stands of this species are also found in the coastal plain of Israel. All the other plants listed above are either semisteppe or Irano-Turanian species.

The association of the RETAMETO-RHUDETUM occupies fairly large areas of the rocky mountain sides which face the lower and central Jordan Valley. The most common components of this association are *Retama raetam* var. *raetam*, *Rhus tripartita*, *Podonosma syriaca*, *Centaurea eryngioides*, *Gymnocarpos fruticosum*, *Echinops blan-*

cheanus, Varthemia iphionoides, Carlina corymbosa, Gypsophila rokejeka, and *Carthamus nitidus.*

Retama raetam is a species most variable chiefly in its fruits. It is a broomlike shrub, 1–2 m. high, with small and early caducous leaves, white flowers, and ovate, one-seeded, indehiscent fruits. The range of distribution of this variety extends all along the Sahara to Arabia and the upper Jordan Valley. It is the "rotem" of the Bible, and one of the most characteristic plants of Palestine's deserts.

The PHLOMIDETUM BRACHYODONTIS association occurs chiefly in the Judean Desert and is likewise confined to rocky habitats. *Phlomis brachyodon,* the dominant plant, is associated with *Poa eigii, Carex pachystylis, Noëa mucronata, Salsola vermiculata* ssp. *villosa, Echinops blancheanus, Artemisia herba-alba, Lactuca orientalis, Varthemia iphionoides,* and *Linaria aegyptiaca.* There is also a series of Mediterranean and Irano-Turanian annuals.

The ARTEMISION HERBAE-ALBAE alliance includes a series of plant communities which are dominated and characterized chiefly by *Artemisia herba-alba* (see Fig. 31). This sagebrush is one of the most typical plants of the western part of the Irano-Turanian region. It is a fragrant, gray, hairy dwarf shrub, with shallow roots and small pinnatifid leaves. It flowers and fruits in early winter. Its general range of distribution extends from Spain through the North African steppes to anterior Asia. In the area under review it occupies large stretches of the Irano-Turanian territory in the Negev, the Judean Desert, and Transjordan.

The associations of this alliance are quite well differentiated from each other, both in their composition and the edaphic conditions of their respective habitats, e.g., rocks, gray calcareous soils, loess, and sands. The following is one of the records taken of the ARTEMISIETUM HERBAE-ALBAE TYPICUM (Fig. 38), occurring in the central Negev on gray calcareous soils of the rocky hillsides south of Avdat, about 800 m. above sea level:

Artemisia herba-alba
Reaumuria palaestina
Gymnocarpos fruticosum
Helianthemum ventosum
H. vesicarium
Convolvulus oleifolius
Moricandia nitens
Astragalus amalecitanus
A. sanctus
Noëa mucronata
Echinops spinosissimus
Poa sinaica
Carex pachystylis
Phagnalon rupestre
Erodium hirtum
Scorzonera judaica
Stipa szowitsiana
Tulipa amblyophylla

There are others in addition to this list.

The main association of the HALOXYLION alliance, the HALOXYLETUM ARTICULATI (Fig. 39), occurs in the Negev, Sinai, and Trans-

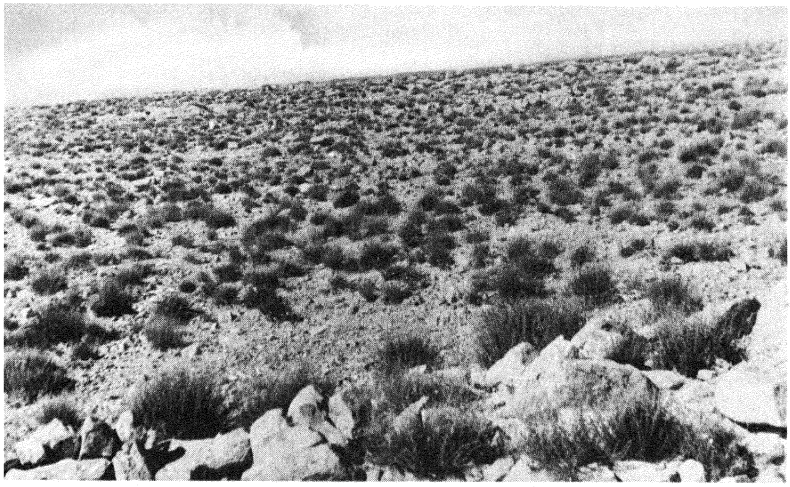


Fig. 38. *Artemisietum herbae-albae*, near Avdat, Negev.

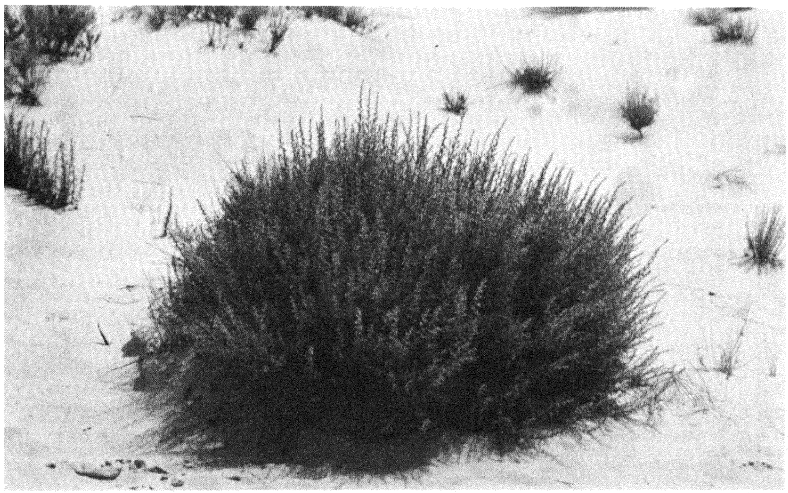


Fig. 39. *Haloxyletum articulati*, fluviatile loess, environs of Revivim, Negev.

jordan. It is largely confined to heavy fluviatile loess soil of wadi terraces and lowlands with a soil salinity of 1 per cent or so. The distribution range of *Haloxylon articulatum* (Fig. 40) is similar to that of *Artemisia herba-alba*. It is a succulent, leafless, articulate dwarf shrub with a much-branched, vertical or spreading root sys-

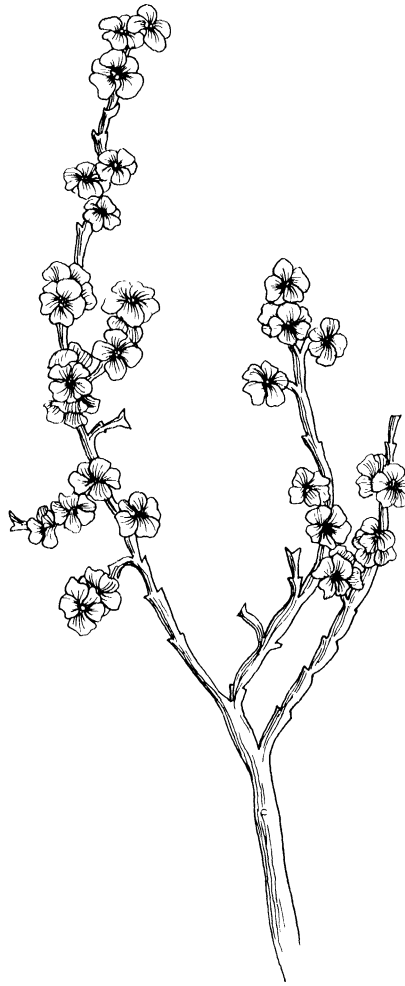


Fig. 40. *Haloxylon articulatum.*

tem. It flowers and its fruits ripen in autumn or early winter. Since the sites of HALOXYLETUM ARTICULATI are sporadically cultivated by Bedouins, this association also comprises, apart from *Haloxylon*, some segetals and desert "wides" such as *Stipa tortilis*, *Malva aegyptia*, *Trigonella arabica*, *Avena wiestii*, *Astragalus callichrous*, *Plantago ovata*, *Enarthrocarpus strangulatus*, *Ifloga spicata*, *Aizoon hispanicum*, etc.

Another association of this alliance, also more or less segetal in character, is that dominated by *Anabasis haussknechtii*. It occurs both on loess or loesslike soil of the Negev and in the highlands south of Amman. In the latter the following species accompany *Anabasis: Poa sinaica, Carex pachystylis, Scrophularia deserti, Colchicum ritchii, Leopoldia longipes, Astragalus platyraphis, etc.*

The Saharo-Sindian Vegetation

Large expanses of hammada, salines, sand dunes, and the almost complete lack of cultivation are characteristic features of the Saharo-Sindian territory. Despite the extremes of the climatic and edaphic conditions, the vegetation is differentiated into a considerable number of plant communities mainly belonging to four classes: the RETAMETEA ARENARIA, occupying coastal dunes and sand fields; the SUAEDETEA DESERTI, comprising the halophytic vegetation; the ANABASIDETEA ARTICULATAE, comprising mainly the hammada vegetation; and the HALOXYLOTEA SALICORNICI, characteristic of interior sand dunes and sandy soils. The vegetation of the latter two classes will be dealt with here and the others will be discussed in the next chapter.

The Anabasidetea Class. The following is a list of plant communities (Eig, 1946) included in this class:

ZYGOPHYLLETALIA DUMOSI ORDER

1. ZYGOPHYLLION DUMOSI alliance
   a. ZYGOPHYLLETUM DUMOSI
   b. GYMNOCARPETUM FRUTICOSI
2. CHENOLEION ARABICAE alliance
   a. *Erodium glaucophyllum–Herniaria hemistemon* assoc.
   b. CHENOLEETUM ARABICAE
   c. *Chenolea arabica–Salsola villosa* assoc.
   d. ATRIPLICETUM PALAESTINAE
   e. REAUMURIETUM PALAESTINAE
3. SUAEDION ASPHALTICAE alliance
   a. SUAEDETUM ASPHALTICAE
4. SALSOLION VILLOSAE alliance
   a. *Salsola villosa–Gymnocarpos fruticosum* assoc.
   b. SALSOLETUM TETRANDRAE
   c. SALSOLETUM VILLOSAE
   d. *Anabasis articulata–Notoceras bicorne* assoc.
   e. *Salsola villosa–Stipa tortilis* assoc.

ANABASIDETALIA ARTICULATAE ORDER

1. ANABASIDION ARTICULATAE alliance
   a. *Anabasis articulata–Retama raetam* assoc.

b. *Anabasis articulata–Zilla spinosa* assoc.
c. ANABASIDETUM ARTICULATAE TYPICUM

The ZYGOPHYLLETUM DUMOSI (Fig. 41) is the most important plant community of the desert. It inhabits hammada and hammada-like hills and hillsides which are interrupted by plains and wadis in the

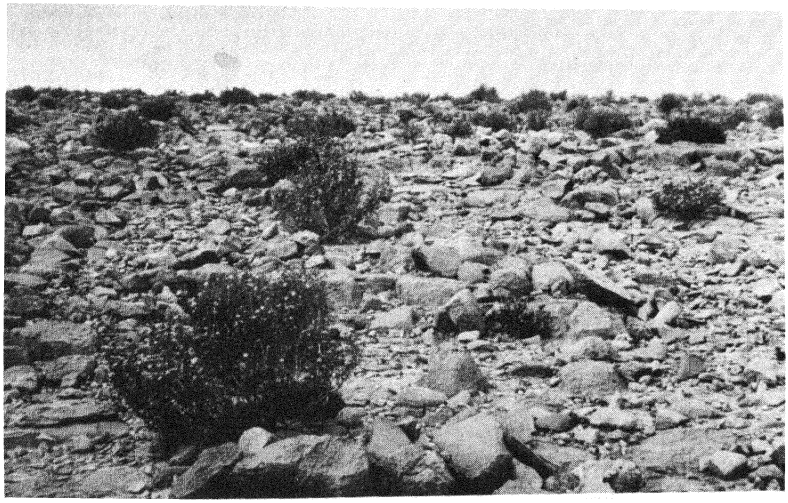


Fig. 41. *Zygophylletum dumosi*, hammada, between Meishor Yemin and the Dead Sea, Negev.

northern and central Negev. The floristic composition of this association is well characterized by the following species:

Zygophyllum dumosum
Gymnocarpos fruticosum
Reaumuria palaestina
Noea mucronata
Astragalus spinosus
Traganum nudatum
Atractylis serratuloides
Halogeton alopecuroides
Salsola tetrandra
Helianthemum kahiricum
Diplotaxis harra
Herniaria hemistemon
Scorzonera judaica
Salsola inermis
Aegilops kotschyi
Erodium lacinatum
E. hirtum
Rumex roseus
Astragalus tribuloides
Plantago ovata
Gymnarrhena micrantha
Asteriscus pygmaeus
Stipa tortilis
Reboudia pinnata
Scabiosa aucheri
Sclerocaryopsis spinocarpos
Carrichtera annua
Trigonella stellata

The ZYGOPHYLLETUM grows in the Negev on gravelly or stony hillsides with an annual rainfall of only 100–75 mm. South and east of the area occupied by this plant community the amount of rainfall

decreases and vegetation persists only in the lowlands where the scantiness of atmospheric moisture is compensated for by run-on or underground moisture. The ZYGOPHYLLETUM comprises a large number of winter annuals which appear only in rainy years. The perennials are mainly succulent chamaephytes which replace their larger winter leaves by minute summer leaves. This replacement enables them to remain physiologically active also during the dry season. In *Zygophyllum* (Fig. 42) the shedding of leaflets results in a surface reduction that may amount to 87 per cent, i.e., only about 13 per cent of winter surface is exposed during the summer season. Other chamaephytes, too, reduce their summer transpiration surface but to a lesser degree. M. Zohary and Orshan (1954) have shown that the ZYGOPHYLLETUM cannot maintain its activities in summer, unless the annual associates disappear and the perennials reduce their transpiration intensity and diminish considerably the surface of their transpiring organs.

The ZYGOPHYLLETUM occurs in the Negev in two variants. One is confined to hammada hills covered with flint stones where the subsoil consists of a fine mealy and gypseous matter intermingled with gravel and containing up to 2 per cent of soluble salts. In the second variant, the plants are confined to fissures and interspaces of a rocky substratum in which gray and less saline soil accumulates. This latter variant mainly occupies the eastern portion of the central Negev and is characterized, among others, by the occurrence of *Farsetia aegyptiaca, Asparagus stipularis, Statice pruinosa,* and others as frequent associates of *Zygophyllum.*

Closely allied to the ZYGOPHYLLETUM in regard to its ecology and floristic features is a series of plant communities confined to soft gypseous soils. An example is CHENOLEETUM ARABICAE, with *Chenolea arabica* as a leading plant, which is very often accompanied by *Halogeton alopecuroides, Helianthemum kahiricum, Reseda muricata, Erodium hirtum, Herniaria hemistemon, Aaronsohnia faktorovskyi,* and others. Another community is SUAEDETUM ASPHALTICAE (Fig. 43), in which *Suaeda asphaltica,* the dominant plant, is accompanied by desert annuals. In both communities the leading plants are dwarf shrubs with small succulent leaves, shallow root systems, and high osmotic values. They are abundant on gypsiferous rocks of the Senonian (Danian and Maestricht) strata of the Judean Desert and Transjordan.

On marls and other soft limestone substrata of the Judean Desert and Dead Sea region the SALSOLETUM VILLOSAE and SALSOLETUM TETRANDRAE are encountered. The leading plants of both are small-leaved chamaephytes, tolerating exposure to severe drought and

Fig. 42. *Zygophyllum dumosum.*

fairly high degrees of salinity in their soils They are highly adaptable to drought, and in a dry year they can reduce their new growth to zero and stand almost leafless for one or more years. They are accompanied by many winter annuals, occurring only in rainy years.

Of the order ANABASIDETALIA the *Anabasis articulata–Retama raetam* association is confined to the sandy plain of Tureiba (Meishor Yemin) of the central Negev. The sands here are formed *in situ* and

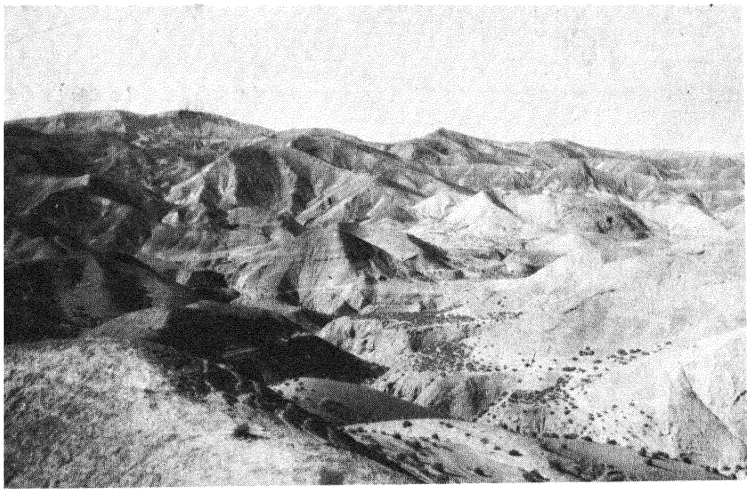


Fig. 43. *Suaedetum asphalticae,* on gypseous ground, near El Quneitra, Judean Desert.

derive from a Neogene sandstone. A sample record taken from this association comprises the following species: *Anabasis articulata, Retama raetam, Thymelaea hirsuta, Artemisia monosperma, Verbascum fruticulosum, Atractylis flava, Helicophyllum crassipes, Ornithogalum trichophyllum, Asphodelus microcarpus, Aristida obtusa, A. ciliata, Pancratium sickenbergerii, Matthiola livida, Lotus villosus, Schimpera arabica, Adonis dentata,* and many others.

The dominant plant, *Anabasis articulata* (Fig. 44), is a deep-rooting, articulate, leafless, succulent plant. *Retama* is an evergreen, spartoid shrub, also with a deep root system; it sheds its leaves at the end of the rainy season.

Characteristic of the vast stretches of sand fields, which derive from the Nubian sandstone of Lower Cretaceous, is the *Anabasis articulata–Zilla spinosa* association, very common in southern Transjordan. Its coverage is very feeble, and there are almost no annuals.

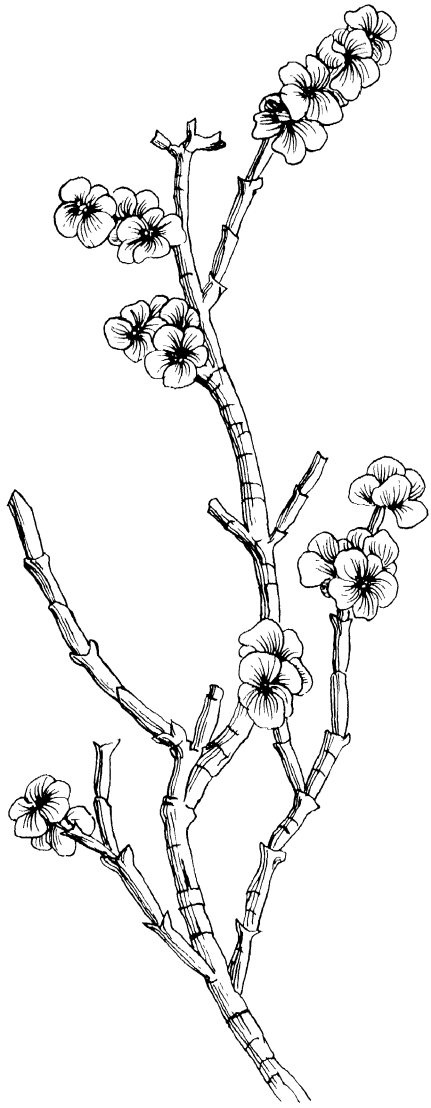


Fig. 44. *Anabasis articulata.*

Among the perennial associates of the community are *Noëa mucronata, Gymnocarpos fruticosum, Retama raetam, Helianthemum ellipticum, Carex pachystylis,* etc.

While the above communities are confined to sandy soils of interior deserts, overlying a hard or stony substratum, there is a third association confined to the wadis, runnels and depressions which cut across the sterile hammadas of the southern Negev, Edom and Sinai. Moisture conditions in such sites are more favorable than those in the immediate surroundings. Moreover, the soil in these beds is more or less leached of its salts, and can thus support a richer flora and vegetation. It is the ANABASIDETUM ARTICULATAE TYPICUM which, apart from *Anabasis,* comprises the following species: *Zilla spinosa, Gymnocarpos fruticosum, Anvillea garcini, Crotalaria aegyptiaca, Salvia aegyptiaca, Fagonia grandiflora, F. kahirina, Farsetia aegyptiaca, Pulicaria undulata, Diplotaxis harra, Reichardia tingitana, Notoceras bicorne,* and *Erodium hirtum.* A series of other annuals also occur. Deeper and broader wadis are often inhabited by *Tamarix* or *Acacia* trees and by *Retama* bushes.

The Haloxylotea Class. This comprises the following two plant associations which are confined to interior desert sand dunes and sand plains.

1. HALOXYLETUM PERSICI (Fig. 45). The predominant plant of this association is *Haloxylon persicum.* In Edom and in the Arava Valley it forms a special type of forest or scrub that is also known from the Aralo-Caspian sand deserts (the "Saxaul forests"), from eastern Persia, and from northern Arabia (Nefud region). *H. persicum,* which here reaches the southern limit of its distribution range, is a rather succulent, spartoid, articulate, many-branched shrub or tree up to 4 m. high with very deep roots. It flowers in spring and has long been subject to misidentification in this region, but it is very well known as the "Ghada" tree of the Arabs, which travelers to Arabia mention as a valuable camel fodder and charcoal plant. Along with *H. persicum* the following plants have been noted: *Calligonum comosum* (Fig. 46), *Retama raetam, Zilla spinosa, Salsola foetida, Farsetia aegyptiaca, Pennisetum ciliare,* and *Eremobium lineare.*

2. HALOXYLETUM SALICORNICI. This association is dominated by *Haloxylon salicornicum,* which is very widespread in the Middle East. It covers vast stretches in the eastern part of Saharo-Sindian North Africa, as well as in Sinai, Arabia, southern Iraq, and Iran.

In Palestine this association is confined to sandy soils or sandy hammadas derived from Nubian sandstone and igneous rocks. It never occurs on coast dunes but on more thermophilous sites of the

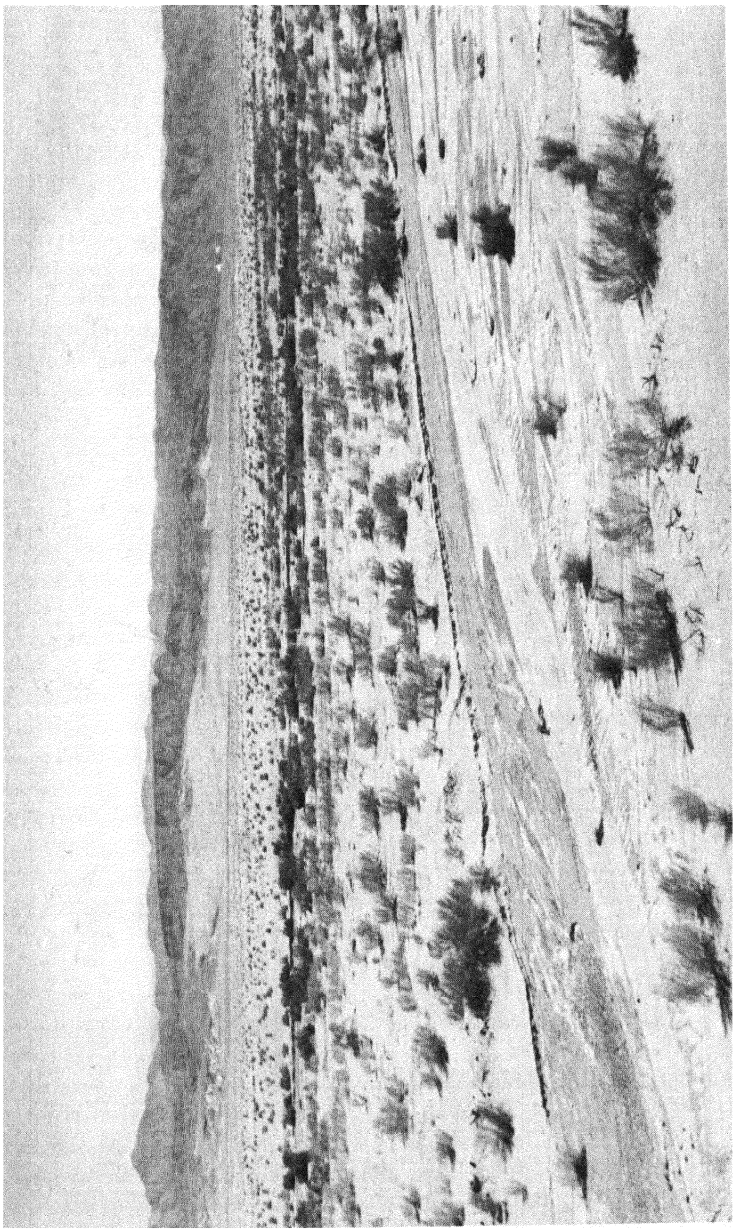


Fig. 45. *Haloxyletum persici*, Nubian sandstone sands, near Yotvata, southern Arava Valley.

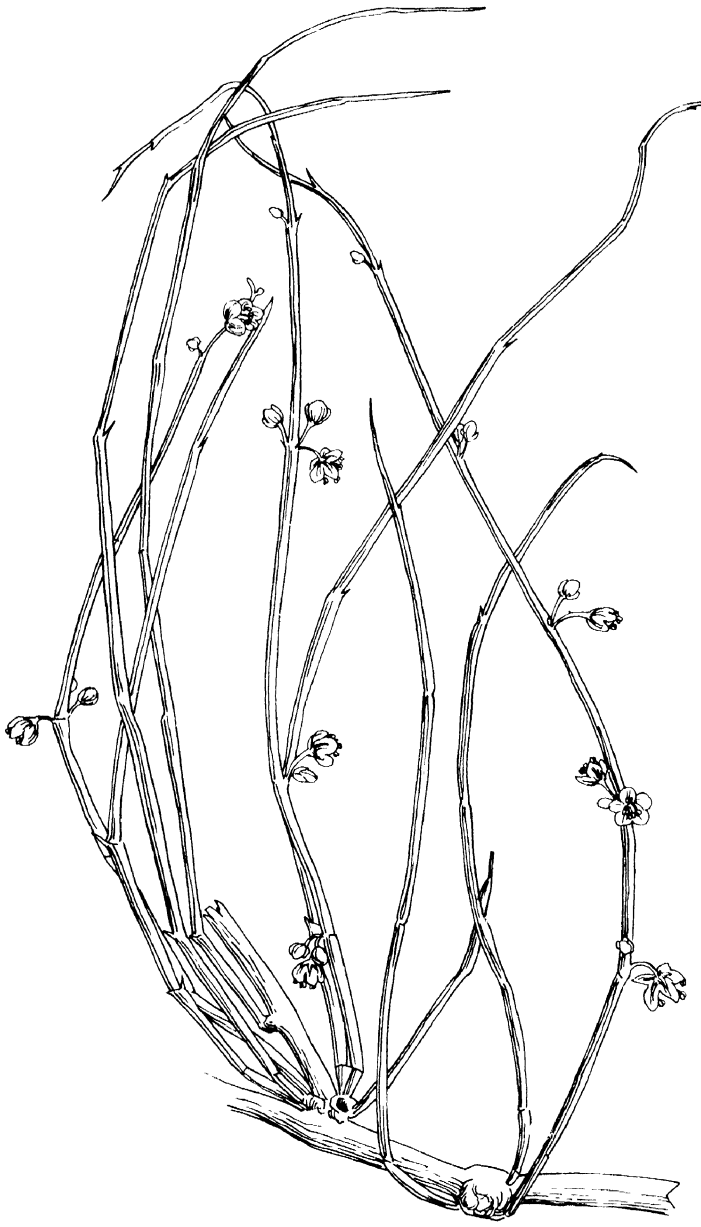


Fig. 46. *Calligonum comosum*

interior deserts. The following species make up the composition of this association in the southern part of the Arava Valley near Timna:

Haloxylon salicornicum
Panicum turgidum
Crotalaria aegyptiaca
Aristida obtusa
Monsonia nivea
Fagonia bruguieri
Salvia aegyptiaca
Citrullus colocynthis
Aerva tomentosa
Robbairea prostrata
Salsola foetida
Schismus barbatus

Haloxylon salicornicum is a leafless, succulent, articulate dwarf shrub very similar to *Anabasis*. It flowers in late autumn and fruits in early winter.

The Tropical Vegetation

In the area under review there are about 60 species belonging to various tropical floras; most important among them is the Sudanian element. Historically, as has been pointed out in an earlier chapter, these plants are relics of a Tertiary tropical flora, which probably dominated larger parts of the area up to the Late Miocene. After its decline during the Pliocene, the remains of this flora took refuge mainly in the lower Jordan and the Arava valleys. The relatively high winter temperatures and the ground-water bodies occurring here in the outlet regions of permanent and ephemeral watercourses are most favorable to the maintenance of this element. We encounter this tropical flora throughout the lower Jordan–Arava rift valley, in a chain of greater or smaller oases that stand in marked contrast to the desolate desert surroundings. These tropical oases, which represent northernmost outposts of African tropical vegetation in anterior Asia, are Ein Gedi, Jericho, Wadi Far'a, Ghor es Safi, Wadi Nimrim, Yabbok River, etc.

The following are the most important trees and shrubs of this flora: *Acacia negevensis, A. raddiana* (Fig. 47), *A. tortilis* (Fig. 48), *A. laeta, Hyphaene thebaica* (Fig. 49), *Moringa aptera, Salvadora persica, Zizyphus spina-christi* (Figs. 50, 51), *Calotropis procera, Balanites aegyptiaca, Sebestena gharaf, Grewia villosa, Maerua crassifolia, Abutilon muticum, A. fruticosum, Solanum incanum* and *Cassia obovata*. The plant communities formed by these plants are generally fragmentary. To a large extent they have been destroyed by man, who has cultivated the sites of this tropical vegetation since time immemorial.

Two communities that belong to the class of the ACACIETEA will be mentioned. First the *Zizyphus spina-christi–Balanites aegyptiaca* association is well represented in Ghor es Safi, Ein Gedi, and Nimrim, and is the richest in species. The following species belonging to

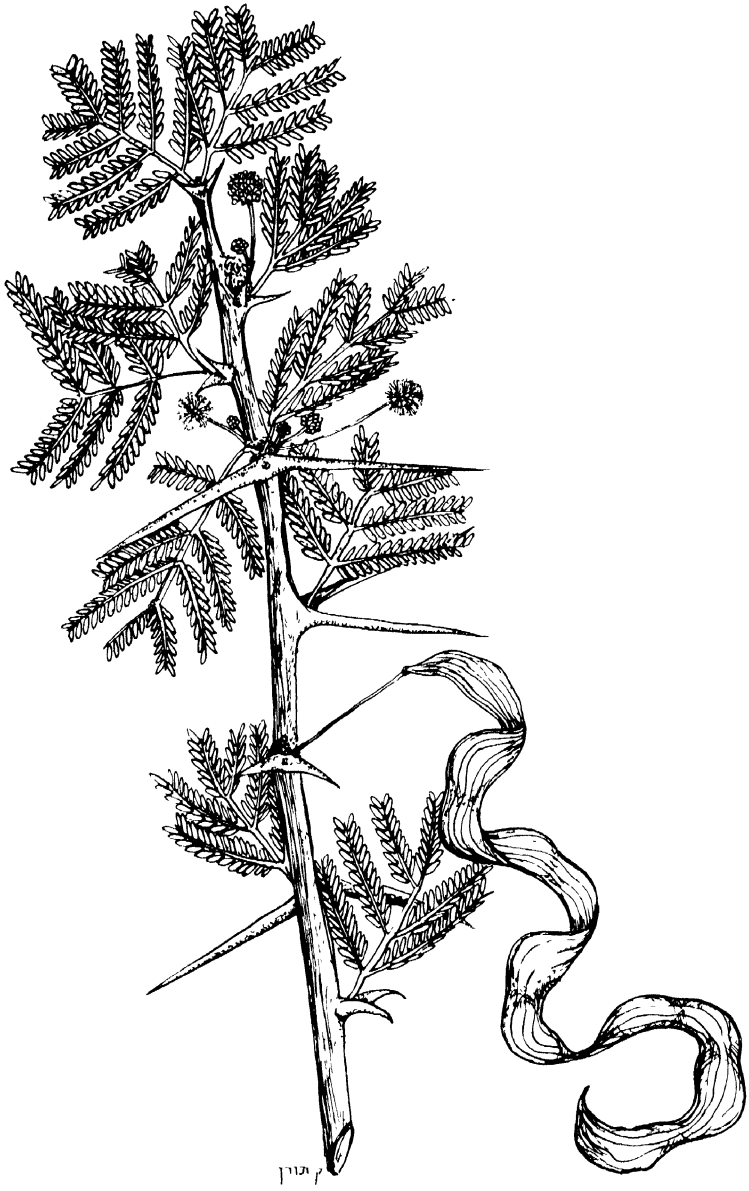


Fig 47. *Acacia raddiana.*

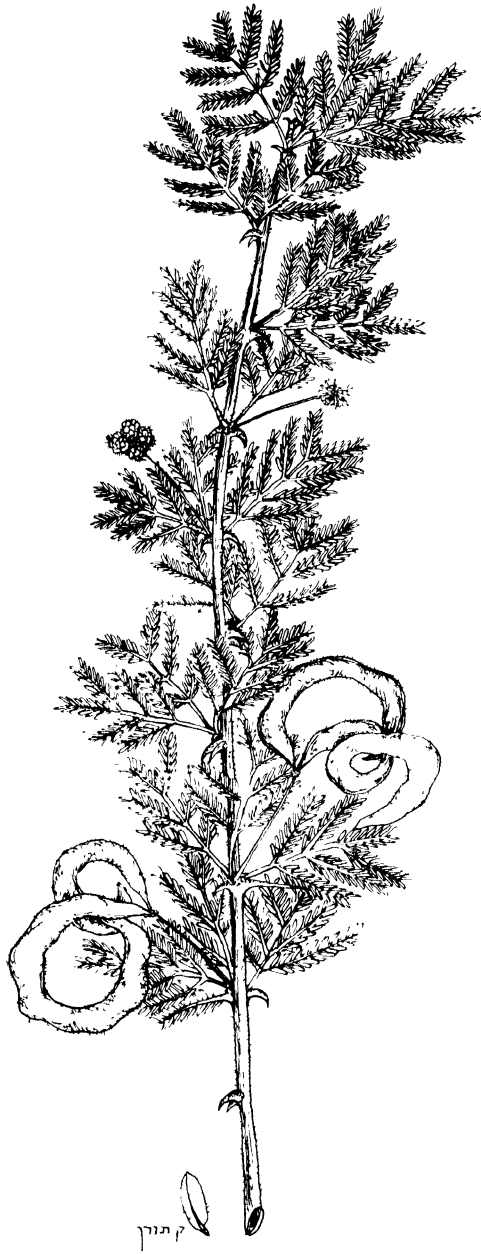


Fig. 48. *Acacia tortilis.*

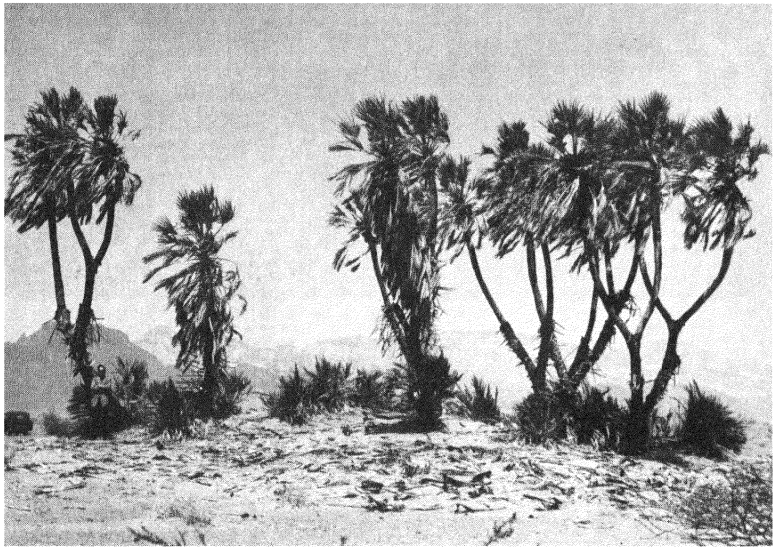


Fig. 49. Stand of *Hyphaene thebaica*, near Eilat, southern Arava Valley.

this association were recorded at Ein Gedi: *Acacia tortilis, A. raddiana, Zizyphus spina-christi, Salvadora persica, Moringa aptera, Grewia villosa, Abutilon muticum, Lavandula coronopifolia, Cassia obovata, Solanum incanum, Calotropis procera, Boerhavia plumbaginacea, Pennisetum ciliare, Balanites aegyptiaca, Suaeda forskalii, Atriplex halimus*, and many others. In the north this association becomes gradually impoverished, so that in the Beit Shean district its only representatives are *Balanites* and *Acacia raddiana.*

Second, the ACACIETUM TORTILIS (Fig. 52), is a more xeric association of tropical vegetation. It is widespread in the Arava Valley and the surrounding tributaries. The leading species of this plant community is *Acacia raddiana*, often accompanied by *A. tortilis*, or in the southwestern part by *A. negevensis.* The shrub layer is dominated by *Anabasis articulata, Haloxylon salicornicum*, or both. Other constituents are: *Gymnocarpos fruticosum, Zilla spinosa, Ochradenus baccatus, Cleome droserifolia, Cassia obovata, Capparis cartilaginea, C. spinosa* var. *negevensis, Lycium arabicum, Daemia cordata, Anvillea garcini, Heliotropium arbainense, Lavandula coronopifolia, Aerva tomentosa, Boerhavia* spp., and many other Saharo-Sindian or tropical dwarf shrubs. Among the annuals, *Anastatica hiero-*

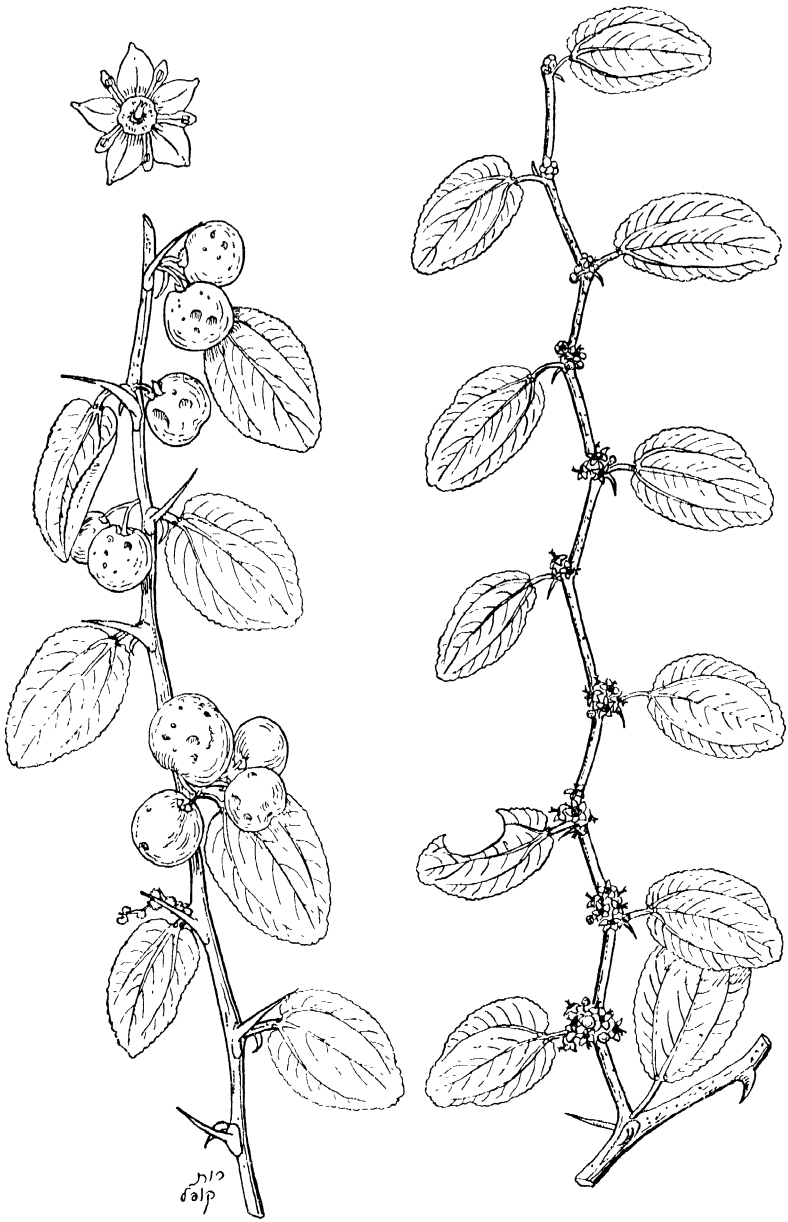


Fig. 50. *Zizyphus spina-christi.*

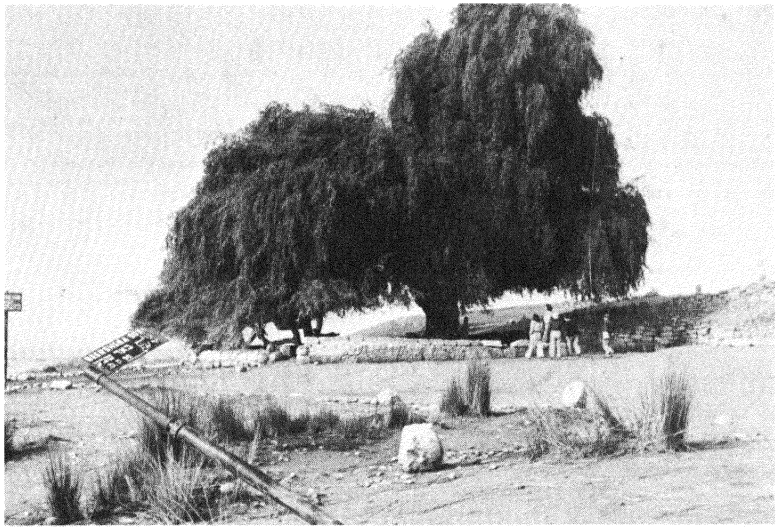


Fig. 51. Aged tree of *Zizyphus spina-christi*, Ein Hatseva, northern Arava Valley.

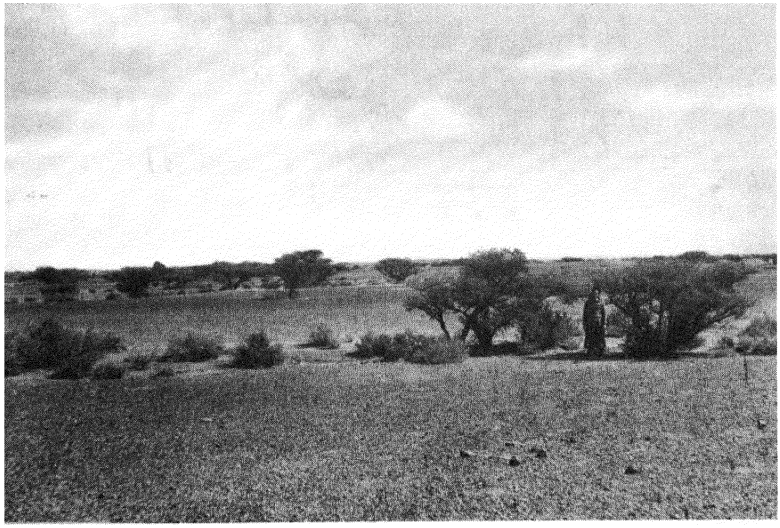


Fig. 52. *Acacietum tortilis* confined to runnels of the barren hammada plains north of Ein Hatseva, northern Arava Valley.

chuntica, *Zygophyllum simplex*, *Senecio flavus*, *Trigonella stellata*, *Erucaria boveana*, and *Reboudia pinnata* are often found. The wadis crossing the sterile hammadas of the Arava Valley are not only sites of the above tropical vegetation but are also survival refuges of rare Saharo-Sindian plants.

It should be noted at this juncture that a few tropical species are also found outside this rift valley. *Zizyphus spina-christi* is also common in the coastal plain. Considerable stands of *Acacia albida* (Fig. 53) are encountered in the coastal plain (e.g., in the districts of

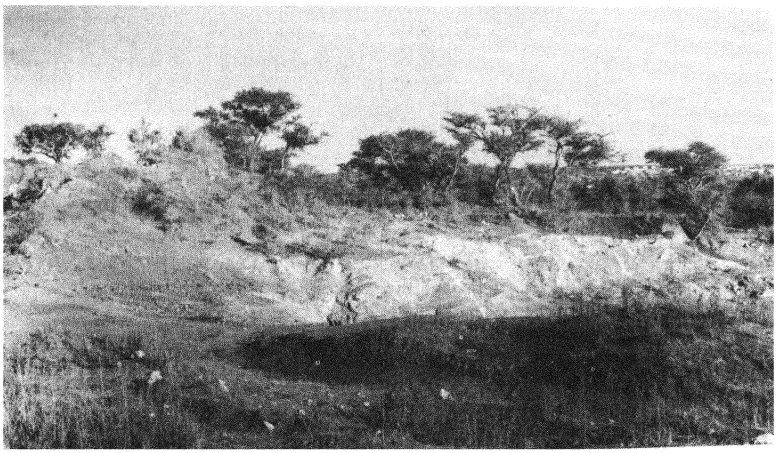


Fig. 53. Stand of *Acacia albida* on basalt soil, Shimron, lower Galilee.

Wadi Sukreir and Ashkelon), in the lower Galilee foothills (Shimron), in the foothills of the Judean Mountains (Emek Haela), further in the Beit Shean district (Wadi Tayibe), and elsewhere. For details on the distribution of this species in Palestine, see Aaronsohn (1913).

7

Vegetation of Coastal Sands, Swamps, and Marshes

These types of vegetation are azonal in the sense that they are less affected by climatic factors of the region than they are by its edaphic features. Hence there is a wide range of distribution of many of their components. Another feature is the arrangement of the vegetation in belting systems; sometimes, however, the contiguous plant communities show marked intergradations into each other. In this case the dominance of one or more species in each respective community must be taken as a key character distinguishing between communities, especially where exclusive character species are altogether lacking.

Vegetation of the Light Soil Belt Along the Coastal Plain

Ecological Remarks. The light soil belt of the coastal plain constitutes a particular entity from the climatic as well as the edaphic point of view. It differs from other parts of Palestine in its flora, vegetation, and ecology. It comprises the coastal sand dunes, the calcareous sandstone soils, locally known as kurkar, the sandy clay soils, and sandy loess. All these soils are poor in nutrient matter and have a low moisture-retaining capacity.

The above-mentioned soil varieties are of Pleistocene origin and are derived, according to geologists, from the sandy supply that is brought in by sea waves and accumulates in dunes as it reaches the shore. The kurkar hills are old, diagenetically consolidated dunes. Under the influence of special climatic conditions this calcareous sandstone has weathered into sandy clay, which, in turn, has undergone decalcification and accumulation of iron and aluminum sesquioxides, which gave rise to hardpan formation in some areas. Geologists believe that the alternating dune piling–kurkar formation and

its weathering to sandy clay is a process that has been repeated several times in the same succession and has resulted in the alternate occurrence of kurkar and sandy clay layers in the profile of these formations (Loewengart, 1928; Picard and Avnimelech, 1937; Avnimelech, 1951). Other theories as to the genesis of the sandstone hills and sandy clay layers have been advanced by Koert (1924), Blake (1935), Rim (1951), and Ravikovitch (1950), but these are less plausible than that put forward here.

The climate of this belt is characterized by comparatively high winter temperatures, by a narrower range of temperature extremes, and by a fairly high percentage of humidity. These environmental qualities affect plant life in several ways. About 150 species occurring here do not grow elsewhere in Palestine. A number of steppe and desert plants grow here side by side with Mediterranean littorals. Many species exhibit particularly deep roots and are equipped with special faculties for fixing mobile sand. Others are resistant to salt spray, calcifugous and thermophilous. There is also a series of widely distributed plants which are represented here by particular ecotypes.

Vegetation. The comparatively large number of plant communities occurring in this belt has been described at length by Eig (1939, 1946), and the ecologic relations of some of them have been studied by M. Zohary (1955) and M. Zohary and Fahn (1951). All the communities are included within the class RETAMETEA ARENARIA. By way of a slight deviation from Eig's classification, the present author subdivides this class further into two orders: the RETAMETALIA ARENARIA PALAESTINA, comprising the associations of the northern part of the coastal plain, and the RETAMETALIA ARENARIA SINAICA, comprising the associations of the Negev part of the coastal plain.

Within the order of RETAMETALIA PALAESTINA the associations are grouped as follows (Eig, 1939):

1. ARTEMISION MONOSPERMAE alliance
   a. *Artemisia monosperma–Cyperus mucronatus* assoc.
   b. *Ammophila arenaria–Cyperus conglomeratus* assoc.
   c. *Lithospermum callosum–Scrophularia hypericifolia* assoc.
2. LOTION CRETICI alliance
   a. *Sporobolus arenarius–Lotus creticus* assoc.
   b. *Ipomoea littoralis–Salsola kali* assoc.
3. DESMOSTACHYON (ERAGROSTION) BIPINNATAE alliance
   a. *Desmostachya (Eragrostis) bipinnata–Centaurea procurrens* assoc.
   b. HELIANTHEMETUM ELLIPTICI
   c. *Ononis stenophylla–Convolvulus secundus* assoc.

The order RETAMETALIA SINAICA comprises:

The RETAMION RAETAM ARENARIUM alliance

a. *Artemisia monosperma–Aristida scoparia* assoc.
b. *Artemisia monosperma–Lolium gaudini* assoc.

VEGETATION OF THE NORTHERN COASTAL SAND DUNES. There is a difference between the vegetation of the low and high shore coasts. On sand dunes of low shores the vegetation is arranged in more or less parallel belts; an example is the sand dunes of the Acre Plain. Here the rather narrow sea-beaten, plantless tidal zone is lined further inland by a shallow, moist sand strip which is characterized by a very fragmentary association of *Ipomoea littoralis–Salsola kali.* Apart from the latter two, it also comprises *Cakile maritima, Euphorbia peplis,* and a few other species, all widely scattered. These annual and succulent plants are all able to withstand sea spray.

The first low front dunes are occupied by the *Sporobolus arenarius–Lotus creticus* association, of which *Agropyron junceum, Pancratium maritimum, Euphorbia paralias,* and *Oenothera drummondii* are characteristic plants. Some of these, especially *Agropyron,* form scattered hummocks. All the components mentioned are highly resistant to sea spray and the roots of most of them reach the saline water level. Still further inland this narrow and often ill-defined zone is lined by a broad belt of the *Ammophila arenaria–Cyperus conglomeratus* association (Fig. 54). In addition to *Ammophila* and *Cyperus,* the association includes the following species: *Silene succulenta, Medicago marina, Scirpus holoschoenus, Tamarix gallica,* and also *Oenothera drummondii, Lotus creticus,* and *Sporobolus arenarius.* The dominant *Ammophila,* which is resistant to spray, is an excellent sand binder on account of its extensively branching root system, and even more, because of its ability to send out new shoots after being buried by onblowing sand and thus to raise the height of the dunes steadily.

Behind the *Ammophila* zone there is an almost plantless strip of shifting sands, varying in width. Behind this plantless strip, further east, there is a broad belt of less mobile or semistabilized sands, occupied by the *Artemisia monosperma–Cyperus mucronatus* association (Fig. 55), which is fairly rich in species. Apart from *Artemisia* and *Cyperus,* it also includes *Polygonum palaestinum, Tamarix gallica, Retama raetam* var. *sarcocarpa, Convolvulus secundus, Medicago marina, Echium angustifolium, Orlaya maritima, Oenothera drummondii, Senecio joppensis, Plantago sarcophylla, Rumex occultans, Trisetum lineare, Cutandia memphitica,* and many others.

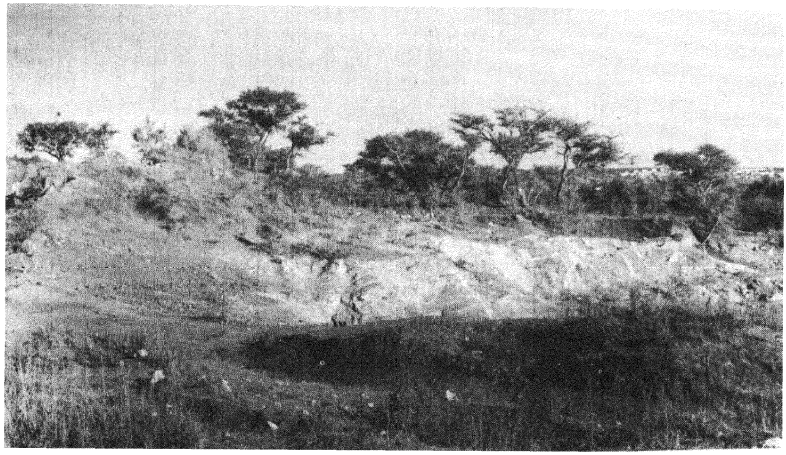


Fig. 54. *Ammophila arenaria–Cyperus conglomeratus* association, dunes, Acre Plain.

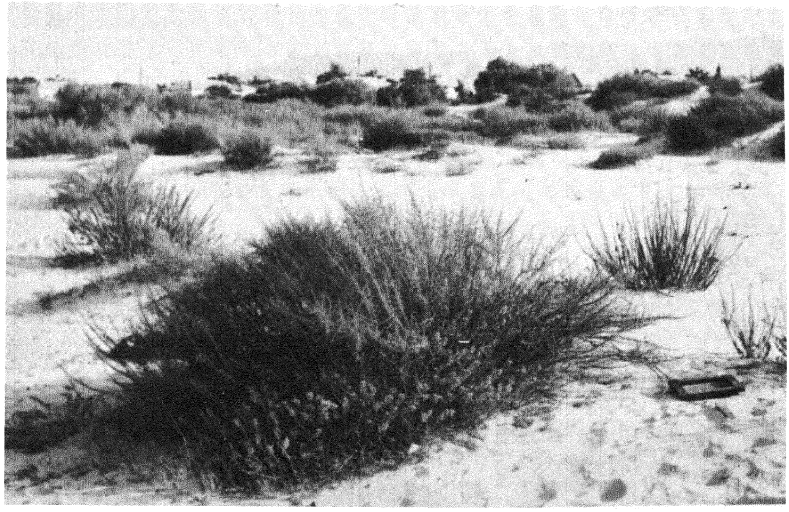


Fig. 55. *Artemisia monosperma–Cyperus mucronatus* association, semi-stabilized dunes near Hadera, Sharon Plain.

Artemisia monosperma, Retama raetam var. *sarcocarpa,* and *Polygonum palaestinum,* the dominant shrubs of this association, are most efficient sand binders, both by virtue of their ability to emerge from the onblowing sand cover, and because they possess exceedingly deep roots (over 10 m. in *Retama* and probably nearly as much in *Artemisia* and *Polygonum*) that withstand the removal of sand from around them. Strong gusts of wind blowing around the plants may destroy the sand hummocks occupied by them but not the plants themselves because they are rooted in the solid substratum underlying the dunes. When exposed by the outblowing action of violent winds, the subterranean parts flatten down and adhere to the surface, into which new lateral roots are sent, so as to allow dune formation starting anew.

The existence of a bare zone between the *Ammophila* and *Artemisia* associations may be interpreted by the assumption that *Ammophila* is unable to occupy this zone because of the prevailing violent wind currents, while *Artemisia* and its associates cannot withstand the sea water spray in this zone, as shown by M. Zohary and Fahn (1951).

On high and steep shores vegetation zones are somewhat differently arranged. As elsewhere, the tidal zone is bare. The steep slope, facing the sea, is occupied by the *Sporobolus-Lotus* association, which is more developed here than on the flat shore. It comprises, in addition to its above-listed components, *Diotis maritima, Crithmum maritimum* (on cliffs), *Inula crithmoides, Statice virgata,* and other plants, all exposed to sea water spray. No sands accumulate on the edge of the high shore plain, and the substratum is built of a solid calcareous sandstone or heavy sandy clay. This solid strip is mainly occupied by the coastal type of POTERIETUM SPINOSI or THYMETUM CAPITATI (dealt with in Chapter 3) or other fragmentary coastal batha communities characterized by *Helianthemum ellipticum, Lithospermum callosum, Salvia lanigera, Thymelaea hirsuta, Statice sinuata, Paronychia palaestina, Atractylis flava, Crucianella maritima,* and others. At a distance from this strip, sands begin to accumulate and pile up into higher dunes occupied mainly by the above-mentioned *Artemisia monosperma–Cyperus mucronatus* association. In addition, there may occur single stands of *Ammophila arenaria,* but the violent winds often result in their destruction. Rarely, such winds attack semifixed dunes, inhabited by *Artemisia* and its associates, and turn the whole area into a wavy sand sea.

VEGETATION OF THE SOUTHERN COASTAL SAND DUNES AND SAND FIELDS. In the south the coastal sand dune belt is wider and higher, the dunes are in full movement, and the vegetation is limited mainly

to sheltered depressions between dunes. The *Artemisia monosperma–Aristida scoparia* association is the most common here. *Panicum turgidum, Pennisetum dichotomum, Convolvulus lanatus,* and some other desert psammophytes lacking in the northern dunes are characteristic components of this association.

A noteworthy habitat of the western Negev is the sandy loess soil in which a rather shallow layer of sand overlies the fine-textured loess soil. This sand cover improves the moisture conditions of loess soil considerably by increasing its capacity to absorb rain water and by decreasing surface evaporation. With no more than 100–150 mm. of annual rainfall, the sandy loess plains are the most fertile areas of the Negev. In fact, almost the whole area here has been under dry farming cultivation since early times. The natural vegetation of this area is predominated by the *Artemisia monosperma–Lolium gaudini* association, in which the wild rye grass gives the landscape a prairie-like appearance. *Lolium* forms only a pioneer stage in this succession and is strongly influenced by cultivation, while *Artemisia* seems to represent the climax stage here. The floristic composition of this association is dealt with in Chapter 9, in connection with segetal vegetation.

At present the mobility of the sand dunes along the entire coastal plain appears to have been increased. This is manifested by the fact that cultivated plots, vineyards, orchards, and buildings are being partly buried by onblowing sand. Moreover, in the northern part of this belt, where part of the consolidated dunes have long ago been inhabited by the climax association of *Ceratonia siliqua* and *Pistacia lentiscus,* violent winds tend to destroy this maquis vegetation and degrade it into the *Artemisia-Cyperus* association, representing an earlier stage in the local successional sere. The harmful influence of wind on dune vegetation may be due to the fact that man has upset the established equilibrium between dunes and vegetation, or to recent increases in wind velocity.

Vegetation of the Kurkar Hills. These consolidated old dunes occur at some distance from the present shore line as discontinuous longitudinal ridges of calcareous sandstone. There are two types of kurkar: one made up of solid and thick layers of calcareous sandstone and the other of thin sand layers alternating with layers of friable calcareous concretions. These types differ from one another in their vegetation. The solid sandstone hills are inhabited chiefly by coastal variants of the Mediterranean dwarf shrub formations (see Chapter 5), such as the associations of *Poterium spinosum–Thymelaea hirsuta, Thymus capitatus–Hyparrhenia* (*Andropogon*) *hirta,* the littoral Cistetum villosi and, north of Natanya, by the *Ceratonia siliqua–*

Pistacia lentiscus maquis. The hills that contain layers of calcareous concretions are generally less favorable to Mediterranean vegetation. They harbor a fairly large number of Saharo-Sindian and Irano-Turanian species and are characterized by the HELIANTHEMETUM ELLIPTICI, the *Ononis stenophylla–Convolvulus secundus* association, and a few others. In the southern part of the coastal plain all these dwarf shrub associations do at times represent the climax vegetation, whereas in the northern part, north of Natanya, the climax association of the kurkar hills is CERATONIETO–PISTACIETUM LENTISCI. The sampling records of the HELIANTHEMETUM ELLIPTICI association taken at Ramat Gan, near Tel-Aviv, included the following plants: *Helianthemum ellipticum*, *Gypsophila rokejeka*, *Heliotropium rotundifolium*, *Scrophularia xanthoglossa*, *Retama raetam*, *Aristida caerulescens*, *Thymelaea hirsuta*, *Salvia lanigera*, *Ononis stenophylla*, *Iris atropurpurea*, *Allium telavivense*, *Alkanna tinctoria*, *Leopoldia maritima*, *Medicago littoralis*, and many other psammophilous annuals.

Fig. 56. *Desmostachya (Eragrostis) bipinnata–Centaurea procurrens* association, sandy clay, Even Yehuda, Sharon Plain.

VEGETATION OF THE SANDY CLAY BELT. The sandy clays are limited to the Sharon Plain and northern Philistia, i.e., to the region between Gedera and Benyamina. The most important and characteristic vegetation unit of this soil is the prairie-like *Desmostachya* (*Eragrostis*) *bipinnata–Centaurea procurrens* association (Fig. 56), which until recently has occupied large parts of the area. The following is

a list of its most common and characteristic species: *Desmostachya bipinnata, Centaurea procurrens, Aegilops longissima, A. sharonensis, Tulipa sharonensis, Nigella arvensis* ssp. *tuberculata, Reseda orientalis, Anchusa aggregata, Brassica tournefortii, Ornithopus pinnatus, Daucus littoralis, Trifolium dichroanthum, T. nervulosum, Lupinus palaestinus, L. luteus, L. angustifolius, Ormenis mixta, Medicago littoralis, M. obscura, Leopoldia maritima, Erodium telavivense, Allium curtum, Silene modesta, S. gallica, Tolpis umbellata, Picris amalecitana, Crucianella herbacea, Corynephorus articulatus, Scabiosa rhizantha, Campanula sulphurea, Lotus villosus, Maresia pulchella, Cutandia philistaea, Trigonella cylindracea, Anthemis leucanthemifolia,* and *Ifloga spicata.*

Desmostachya bipinnata, the dominating bunch grass, is equipped with an intricately branched system of rhizomes which expand horizontally at a depth of 0.5–1 m. over large distances and produce aerial shoots at relatively close intervals. *Desmostachya* is a light-demanding plant and is found as a weed among various crops as well as in young citrus orchards, but it disappears with the growth of the trees. Scattered among the *Desmostachya* grass prairie which until recently occupied most of the surface, are single trees of *Quercus ithaburensis,* clearly indicating that the climax vegetation of at least a part of this belt in the Sharon Plain is a kind of QUERCETUM ITHABURENSIS already discussed above. The *Desmostachya* community was long believed to be syngenetically connected with the *Quercus* forest (Eig, 1939), but thorough investigation has shown that the Sudanian *Desmostachya* is a more recent invader of the forest district, and that its main expansion took place only after the destruction of the oak forest by man. The latter seems to develop through the successional sere of Mediterranean dwarf shrub communities, dealt with in Chapter 5. At present this belt of sandy clay soils has become a center of local intensive agriculture, especially of citrus-growing, and natural vegetation is rapidly disappearing.

The Hydrophytic Vegetation

The two centers of hydrophytic vegetation in Palestine are the coastal plain and the Jordan Valley. Several permanent rivers, pouring out into the Mediterranean Sea, traverse the coastal plain. Time and again dunes and kurkar hills along the shore line have obstructed the free outpour of these rivers into the sea. This has resulted in an inundation of vast areas and the formation of swamps in the vicinity of water currents in the coastal plain. In the Jordan Valley there are the Huleh swamps and the Lake of Huleh and their affluents, as well

as the banks of the Jordan River and its tributaries, which offer a variety of habitats to hydrophytic plant life.

While most local hydrophytes have their origin in northern temperate regions, there are also a fair number of tropical origin. Among the latter the following are noteworthy: *Marsilia diffusa, Cyperus papyrus, C. latifolius, C. articulatus, C. polystachyus, C. lanceus, C. alopecuroides, Dinebra retroflexa, Paspalidium geminatum, Nymphaea caerulea, Polygonum acuminatum, P. senegalense,* and *Jussiaea repens.* Many species of both the temperate and the tropical group reach their limits of distribution here.

Most of the hydrophytes are at their prime of vegetative development and come into blossom in midsummer. In this dry season this vegetation stands out prominently in the landscape. The hydrophytic vegetation is generally arranged in belts, which, according to their varying conditions of moisture and aeration, create distinct habitats occupied by different plant communities. Other differentiating ecologic factors are duration of the period of inundation, the intensity of wave action, etc.

The author bases his division of the hydrophytic vegetation into associations and higher orders on the methods and principles of European plant sociologists. Accordingly, the following plant sociological units have been distinguished (see also M. Zohary and Orshan, 1947b):

A. Potamotea Class
   a. *Nuphar luteum–Ceratophyllum demersum* assoc.
   b. *Potamogeton lucens–Myriophyllum spicatum* assoc.
   c. Potamogetonetum pectinati
   d. Potamogetonetum fluitantis
   e. Lemnetum minoris

B. Phragmitetea Class
   1. Phragmition mediterraneum orientale alliance
      a. *Cyperus papyrus–Polygonum acuminatum* assoc.
      b. Scirpeto-Phragmitetum
      c. Polygoneto-Sparganietum neglecti
      d. Panicetum repentis
      e. Cyperetum alopecuroidis
   2. Rubion sancti alliance
      a. *Rubus sanctus–Lythrum salicaria* assoc.
      b. Dorycnietum recti
   3. Inulion viscosae alliance
      a. Inuletum viscosae

b. JUNCETUM ACUTI
c. CYPERETUM PYGMAEI
d. LIPPIETO–TRIFOLIETUM FRAGIFERI
e. CRYPSIDETUM MINUARTIOIDIS

4. VERONICION ANAGALLIDIS alliance
a. HYDROCOTYLETUM RANUNCULOIDIS
b. *Veronica anagallis–Nasturtium officinale* assoc.

C. POPULETEA EUPHRATICAE CLASS

POPULETALIA EUPHRATICAE ORDER

1. POPULION EUPHRATICAE alliance
a. POPULETUM EUPHRATICAE
b. TAMARICETUM JORDANIS
c. SALICETUM ACMOPHYLLAE
d. PLATANETUM ORIENTALIS
e. FRAXINETUM SYRIACAE (fragments)

NERIETALIA OLEANDRI ORDER

1. NERION OLEANDRI alliance
a. VITICETUM AGNI-CASTI
b. NERIETUM OLEANDRI
c. ARUNDINETUM DONACIS

The Potamotea Class. This comprises the higher vegetation of ponds and lakes and also that of slow water currents. The associations of this class are fragmentary and rather rare in Palestine. They are each represented by only one or two species. The *Potamogeton lucens–Myriophyllum spicatum* association thrives in deeper waters, while that of *Nuphar luteum–Ceratophyllum demersum* occupies shallow and rather stagnant water bodies. POTAMOGETONETUM FLUITANTIS is found, as a rule, in slow-flowing streams. *Lemna minor* and *L. gibba* associations are often encountered in shady ditches.

The Lake of Huleh, which has been drained and is about to disappear, has until recently been one of the largest centers of this class. *Nymphaea alba* and *N. caerulea* have become exceedingly rare of late. However, the ever-increasing number of artificial fish ponds offer new sites for the vegetation of this class.

The Class Phragmitetea. This comprises the following alliances:

THE PHRAGMITION MEDITERRANEUM ALLIANCE. The most common association of this alliance is SCIRPETO-PHRAGMITETUM. It is characteristic of low banks of permanent rivers and streams, and of periodically submerged swamps. Its dominant species in the region under discussion are *Phragmites communis* var. *isiacus* and *Typha angustata* (sometimes only either one or the other). They either occur

in pure stands or are accompanied by other plants, such as *Cyperus longus*, *Panicum repens*, *Scirpus lacustris*, *S. littoralis*, *Polygonum nodosum*, *Cladium mariscus* (very rare), and others.

Particularly interesting is the association of *Cyperus papyrus–Polygonum acuminatum* (Fig. 57), which occupies large stretches in flooded peat soils of the Huleh swamps. It occurs in a few variants and comprises, apart from the two dominating species, *Galium elongatum*, *Roripa amphibia*, *Dryopteris thelypteris*, and sometimes

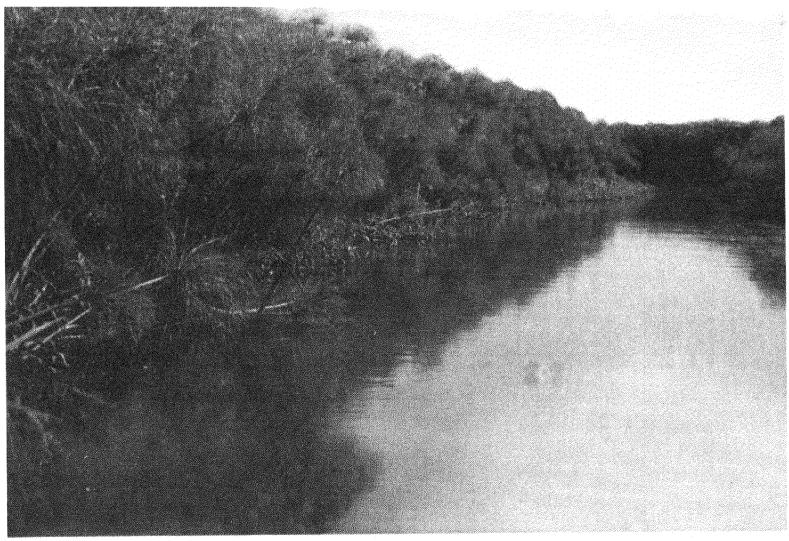


Fig. 57. *Cyperus papyrus–Polygonum acuminatum* association, Huleh swamps, Huleh Plain.

also *Urtica hulensis*, *Lycopus europaeus*, *Polygonum senegalense*, *Alternanthera sessilis*, and others. *Cyperus papyrus* is also known in certain swamps elsewhere in Palestine, e.g., in the Ata Pond near Hadera or on the banks of the Yarkon and Alexander rivers. This plant has long been used for the manufacture of mats, an industry which has supported many families living near the swamps.*

The POLYGONETO-SPARGANIETUM NEGLECTI forms a considerable belt in the Huleh swamps but also occurs on river banks elsewhere. In a typical stand of this association the following species have been

* Although the largest part of the Huleh swamps has very recently been drained and most of its vegetation largely destroyed, the records on the zonation of this vegetation may be at least of historical interest.

noted: *Sparganium neglectum, Cyperus lanceus, Iris pseud-acorus, Marsilia diffusa, Polygonum acuminatum, P. scabrum, Jussiaea repens, Panicum repens, Typha angustata, Butomus umbellatus,* and others.

PANICETUM REPENTIS is fairly common on river banks and in flooded lowlands. In the Huleh Basin, for example, it forms the outer belt of the swamp vegetation. PANICETUM REPENTIS is accompanied here by *Scirpus maritimus, Alisma plantago-aquatica, Echinochloa crus-galli, Jussiaea repens,* etc.

THE RUBION SANCTI ALLIANCE. The most important member of this alliance is the *Rubus sanctus–Lythrum salicaria* association, found on elevated banks of permanent or ephemeral rivers as well as on swamp borders. In addition to the two dominant species it comprises *Cynanchum acutum, Epilobium hirsutum, Saccharum aegyptiacum, Convolvulus saepium, Cyperus longus, Dorycnium rectum, Pulicaria dysenterica, Verbena officinalis, Eupatorium cannabinum, Salix acmophylla,* and others.

THE INULION VISCOSAE ALLIANCE. This comprises a few associations whose habitats become flooded during winter but dry up in early summer. Unlike the RUBION SANCTI alliance it comprises a large number of annuals. JUNCETUM ACUTI is frequently found as the outermost belt in the vegetation of river banks that are flooded only sporadically, but it is indicative of a high ground-water table. The following plants are frequently encountered in this association: *Juncus acutus, Pulicaria dysenterica, Teucrium scordioides, Stachys viticina, Festuca arundinacea, Carex* spp., *Lotus tenuifolius, Oenanthe prolifera, Mentha pulegium, Centaurium spicatum, Cynodon dactylon,* and others.

The INULETUM VISCOSAE is ecologically and floristically very close to the latter association but is much more common in Palestine, and also occurs as isolated stands in slight depressions of heavy, undrained land. *Inula* is often accompanied by *Verbascum sinuatum, Stachys viticina, Verbena officinalis, Xanthium strumarium,* and other swamp plants.

CRYPSIDETUM MINUARTIOIDIS is an association comprising only a few annuals, such as *Crypsis minuartioides, Heliotropium supinum, Glinus lotoides, Pulicaria arabica, Verbena supina,* and *Chrozophora plicata.* It is confined to slight depressions that are inundated in winter and dry out in summer.

THE VERONICION ANAGALLIDIS ALLIANCE. This alliance comprises a series of minor and sometimes fragmentary associations occupying permanent brooklets, the margins of springs, and the like. *Veronica*

anagallis-aquatica is found accompanied by *Nasturtium officinale, Apium graveolens, Mentha incana, Helosciadium nodiflorum, Cyperus fuscus, Fimbristylis ferruginea,* and others.

* * *

The zonal arrangement of hydrophytic vegetation is well illustrated by a transect made in the Huleh swamp (Fig. 58), one of the largest swamps in the Near East, the vegetation of which has recently been studied by Jones (1940) and M. Zohary and Orshan (1947b). Crossed by two main watercourses, the Jordan and the Turra, and fed by a large number of local springs, this area is periodically flooded. The center of the swamp, consisting of alkaline, submerged peat, is occupied by the *Cyperus papyrus–Polygonum acuminatum* association. This association is surrounded by a belt of SCIRPETO-PHRAGMITETUM growing on mineral soil and enclosed concentrically by POLYGONETO-SPARGANIETUM, while the INULETUM VISCOSAE and JUNCETUM ACUTI constitute the outer fringes of this vegetation complex. Soil composition and length of the inundation period are the main factors responsible for this belting. The floristic interest of the Huleh swamps does not lie in their extraordinary abundance in species only, but also in the fact that they constitute a meeting place of Tropical African and boreal hydrophytes.

At the time of writing this chapter, large-scale draining operations are about to turn this swamp into a highly fertile agricultural area. Many of the local wild plants have already disappeared, e.g., *Marsilia diffusa, Utricularia vulgaris, Wolffia arrhiza, Lemna* spp., *Hydrocharis morsus-ranae,* and others. A reservation plot of sufficient size has been left undrained to safeguard wild life and flora from total destruction.

* * *

The Populetea Class. This comprises riparian woods and scrub vegetation. It has been subdivided into the following two alliances.

THE POPULION EUPHRATICAE ALLIANCE. On the banks of the Jordan River and the tributaries pouring into the Jordan and the Dead Sea, POPULETUM EUPHRATICAE and TAMARICETUM JORDANIS (Fig. 59) form dense and sometimes even impenetrable woods. They adorn the bare and desolate surroundings with an evergreen meandering strip. While *Populus* occupies the frontal part of the bank, *Tamarix jordanis* is situated mostly behind it. Sometimes both associations merge together. In the shade of these trees one often encounters *Lycium europaeum, Atriplex halimus, Glycyrrhiza glabra, Asparagus*

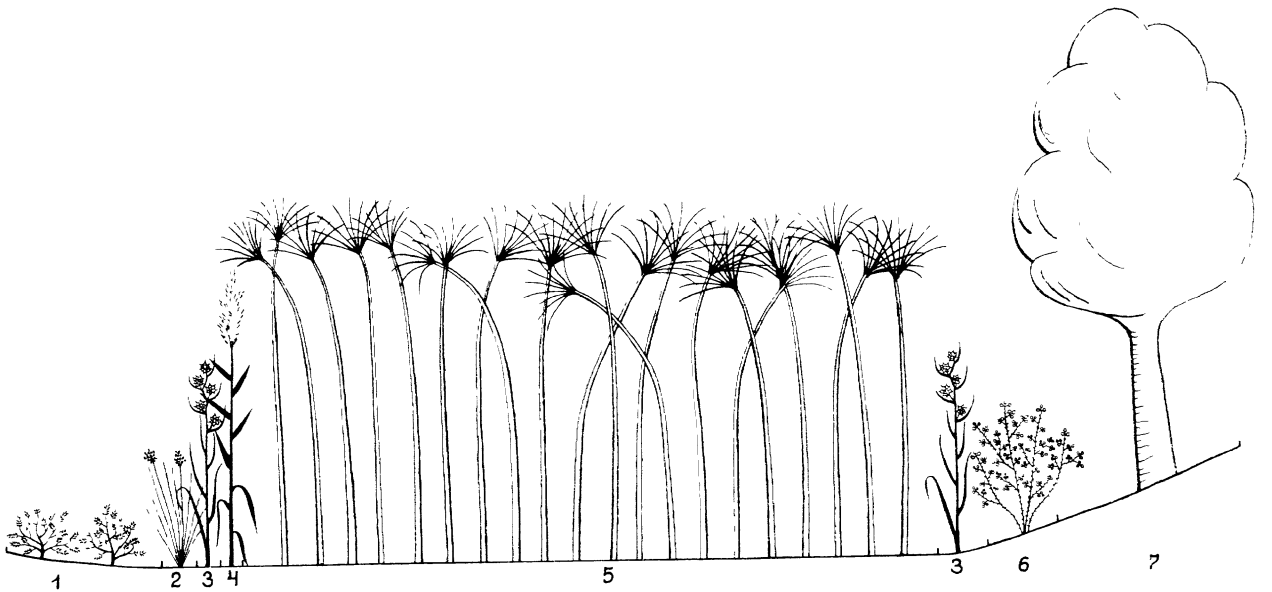


Fig 58. Vegetation transect of the Huleh swamps. Reading from the center of the swamp to the left: 5, *Cyperus papyrus* stands; 4, belt of *Scirpeto-Phragmitetum*, 3, belt of *Polygoneto-Sparganietum*; 2, belts of *Inuletum viscosae* and *Juncetum acuti*; 1, belt of *Scolymeto-Prosopidetum* Reading from the center to the right: 3, belt of *Polygoneto-Sparganietum*; 6, belt of *Rubus sanctus*; 7, scattered trees of *Zizyphus spina-christi*.

palaestinus, *Prosopis farcta*, and others *Prosopis* has its primary habitat here. The plants of these associations tolerate a fairly high amount of soluble salts, which accumulate in summer on the dried-up river sides.

On the banks of the upper part of the Jordan and those of some other rivers both in the mountains and coastal plain, stands of *Salix*

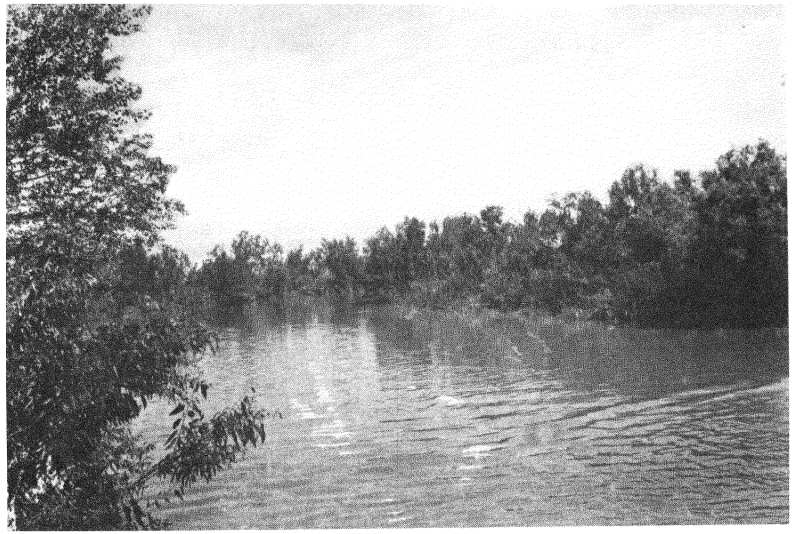


Fig 59. *Tamaricetum jordanis*, banks of the Jordan River, lower Jordan Valley

acmophylla (Fig 60) and *S alba* and a hybrid form of the latter two are occasionally encountered The PLATANETUM ORIENTALIS association is fairly characteristic of the banks of the Jordan River in its northern part It also occurs in upper Galilee on the banks of the rivers Banias, Hasbani, Qani, and others, and aged *Platanus* trees are sometimes found on river banks in the Galilee Mountains Judging from the names of localities in the Judean Mountains, one can assume that this tree also occurred there in the past. Remnants of the riparian *Fraxinus syriaca* forest are found in Tel Dan in the North, in the Beit Shean Valley, as well as on the banks of Nahal Hatannim in the Sharon Plain. There are also a few trees of *Ulmus canescens* on the banks of certain wadis in the Ephraim Mountains They are, no doubt, the last escapists of a past riparian wood.

THE NERION OLEANDRI ALLIANCE. This comprises a few associations growing on stony and gravelly banks or beds of permanent and

ephemeral rivulets both in the mountains and plains. *Nerium oleander* is dominant in one of the associations and *Vitex agnus-castus* in the other. Sometimes both are found growing together. Apart from the dominating *Vitex* or *Nerium*, *Ononis leiosperma*, *Tolpis virgata*, *Inula viscosa*, and *Cephalaria joppensis* have been noted, but these plants are of rather casual occurrence here.

Fig. 60. Stands of *Salix acmophylla*, banks of Hasbani River, upper Galilee.

So much for the plant communities which are the most typical representatives of the local hydrophytic vegetation. Many other communities have not been examined analytically so far, so that the present classification and delimitation of the units must be considered only tentative. The hydrophytic flora and vegetation have recently suffered heavy losses through land reclamations both in the coastal plain and in the Jordan Valley, where large parts of formerly malaria-infested swamps have been drained and turned into most productive agricultural land.

The Halophytic Vegetation

While the hydrophytic vegetation is centered mainly in the Mediterranean territory of Palestine, the bulk of the halophytic vegetation is located in the Saharo-Sindian territory, that is, in the areas surrounding the Dead Sea and in the Arava Valley. A smaller part of it is also found in the vicinity of the Mediterranean coast.

Three types of salines can be distinguished here. inundation salines, formed through flooding of brackish or saline springs and

watercourses; high water table salines; and run-on pan salines. To the first category belong salines of the coastal plain, particularly those of the Acre Plain, fed by the saline water of the Kishon and Na'aman rivers. High water table salines are most abundant in the Dead Sea region and in the Arava Valley, whereas pan salines occurring in closed, undrained lowland basins are scattered in deserts, especially in southern Transjordan. Sodium chloride is the dominating salt in nearly all the salines.

The halophytic vegetation of Palestine falls into two classes—the SUAEDETEA DESERTI of the interior desert salines and the SALICORNIETEA FRUTICOSAE of the Mediterranean coastal plain.

A. The SUAEDETEA DESERTI class comprises the following units:
   1. JUNCO-PHRAGMITION alliance
      a. PHRAGMITETUM COMMUNIS SALINUM
      b. JUNCETUM ARABICI
   2. TAMARICION TETRAGYNAE alliance
      a. *Arthrocnemum glaucum–Tamarix tetragyna* assoc.
      b. TAMARICETUM MARIS-MORTUI
      c. SUAEDETUM MONOICAE
      d. SUAEDETUM FORSKALII
      e. NITRARIETUM RETUSAE
   3. ATRIPLICO-SUAEDION PALAESTINAE alliance
      a. SUAEDETUM PALAESTINAE
      b. SALSOLETUM ROSMARINI
      c. ATRIPLICETUM HALIMI (JORDANIS)
   4. SALSOLION VILLOSAE alliance
      a. *Anabasis articulata–Notoceras bicorne* assoc.
      b. SALSOLETUM TETRANDRAE
      c. *Salsola villosa–Stipa tortilis* assoc.

B. The SALICORNIETEA FRUTICOSAE class comprises the following main units:
   1. THERO-SALICORNION alliance
      a. *Salsola soda–Suaeda splendens* assoc.
      b. SALICORNIETUM HERBACEAE
   2. SALICORNION FRUTICOSAE alliance
      a. TAMARICETUM MEYERI MEDITERRANEUM
      b. *Arthrocnemum glaucum–Sphenopus divaricatus* assoc.
      c. *Salicornia fruticosa–Obione portulacoides* assoc.
   3. JUNCO-PHRAGMITION MEDITERRANEUM alliance
      a. JUNCETUM MARITIMI
      b. PHRAGMITETUM COMMUNIS SALINUM
      c. INULETUM CRITHMOIDIS

The Suaedetea deserti Class. The plant communities of this class have been studied by Eig (1946) and by M. Zohary and Orshan

(1949) in the vicinity of the Dead Sea. This is one of the largest halophytic centers of Palestine, and the following records and observations have been made mainly in this area. The four alliances of this class correspond to the four major habitats:

1. The JUNCO-PHRAGMITION alliance forms a zonation complex of permanently or almost permanently open water bodies. The plants of this alliance are mainly hydrophytes of brackish waters.

2. The TAMARICION TETRAGYNAE alliance includes associations most of which form a belting complex around flooded basins or similar sites subjected to inundation for a longer or shorter period during winter. According to their salt/water relations, they may be looked upon as hydrohalophytes, tolerating both high salinity and submersion of the soil on which they grow.

3. The ATRIPLICO-SUAEDION alliance is confined to habitats which, though not inundated, generally have a high water table. The dominants and codominants of that alliance can be classed according to the salt/water relations of their respective habitats as mesohalophytes, which require or tolerate medium amounts of soil moisture and salt content in the soil but do not tolerate being submerged.

4. The SALSOLION VILLOSAE alliance forms the outermost belt of the whole halophytic vegetation complex. It is confined to driest habitats of the area. The salt content is lower than in any of the other belts, but since moisture content is also very low, the relative concentration of salts is comparatively high. The dominant plants of this alliance may, therefore, be classed as xerohalophytes. The associations included in this alliance have also been listed in the ANABASIDETEA class because of their transitional nature.

Of associations belonging to the JUNCO-PHRAGMITION alliance, those of *Phragmites communis* and *Juncus arabicus* are confined to banks of streams, runnels, springs, and ponds containing muddy or brackish water throughout the whole year or part of it. They form almost pure stands and are often arranged in parallel belts with *Phragmites* closest to the water source. *Juncus* is sometimes accompanied by *Statice limonium, Inula crithmoides, Aeluropus littoralis, Suaeda baccata, S. forskalii* (=*S. fruticosa* Forsk.), and others. The above communities are related both ecologically and floristically to *Phragmites* and *Juncus* associations of the SALICORNIETEA class, and form a bridge between the two classes.

The association of *Arthrocnemum glaucum–Tamarix tetragyna* (Fig. 61) is confined to badly drained depressions and wadis inundated for a certain period in winter. The soil also remains moist after the water level has receded from its surface, so that there is no marked seasonal fluctuation in the soil moisture content, which

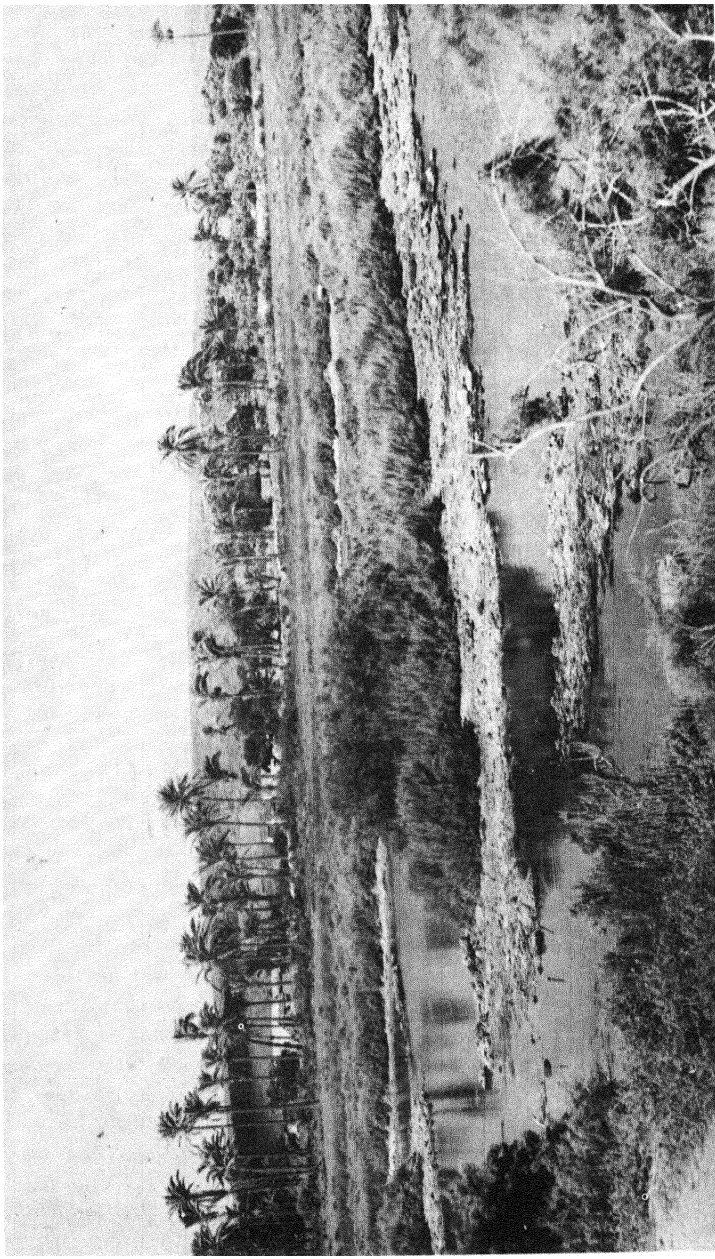


Fig. 61. *Arthrocnemum glaucum–Tamarix tetragyna* association, salt marshes, near Na'aman River, Acre Plain.

ranges from 14 to 23.6 per cent. The percentage of soluble salts, as referred to dry matter, ranges from 5 to 9.5 per cent. The association comprises: *Tamarix deserti, T. gallica* var. *maris-mortui* (Fig. 62), *Arthrocnemum glaucum, Atriplex halimus, Suaeda forskalii, S. palaestina, Mesembryanthemum nodiflorum, Phalaris minor, Sphenopus divaricatus, Aaronsohnia faktorovskyi, Cistanche lutea, Frankenia pulverulenta, Statice spicata,* and *Beta vulgaris.*

The TAMARICETUM MARIS-MORTUI and the SUAEDETUM MONOICAE form almost pure stands of woods in the outlet regions of wadis or in well-drained but permanently flooded depressions. Sometimes they merge into one another to form mixed stands. The dominant trees of this kind are *Tamarix gallica* var. *maris-mortui* or *T. amplexicaulis* and *Suaeda monoica.* They are sometimes accompanied by *Suaeda forskalii, S. palaestina, S. vermiculata, Atriplex halimus,* and others.

The SUAEDETUM FORSKALII occupies broad belts along the bank of the Jordan River at the back of the *Populus euphratica* and *Tamarix jordanis* woods and on the elevated foreshore of the Dead Sea. The dominant species, *Suaeda forskalii,* is also found to penetrate into other associations. It is only occasionally exposed to submersion. The percentage of soluble salts in the soil of the main habitat of this association was found to amount to 1.85 per cent at a depth of 15 cm.

The following species have been noted in association with *Suaeda forskalii* on the banks of the Jordan River near Mathias: *Suaeda baccata, Rumex dentatus, Aeluropus littoralis, Phalaris minor, Sisymbrium irio, Lolium rigidum,* and *Bromus scoparius.* This association is less common along the southern part of the Dead Sea.

The NITRARIETUM RETUSAE covers large areas in the Arava Valley and is also common on the Dead Sea shores. It very often forms the outer fringes of the hydrohalophytic vegetation outlined above. The soil beneath bushes of *Nitraria* has been found to contain as much as 8 to 13 per cent of soluble salts, and has a relatively low moisture content. *Nitraria* is frequently found scattered in widely spaced pure groups. Only rarely is it accompanied by a few dwarf shrubs of *Prosopis farcta, Alhagi maurorum,* and *Statice pruinosa.*

Among the plant communities belonging to the ATRIPLICO-SUAEDION alliance of the Dead Sea region, the SUAEDETUM PALAESTINAE (Fig. 63) is noteworthy in the plain between Jericho and the northern shores of the Dead Sea. The soils it occupies are generally muddy or sodden in winter, dusty and structureless in summer. Their salt content ranges from 1 to 3 per cent, without considerable variations between summer and winter. The species most frequently accompanying the dominant *Suaeda palaestina* are *Mesembryanthemum nodiflorum, Spergularia diandra, Sphenopus divaricatus,*

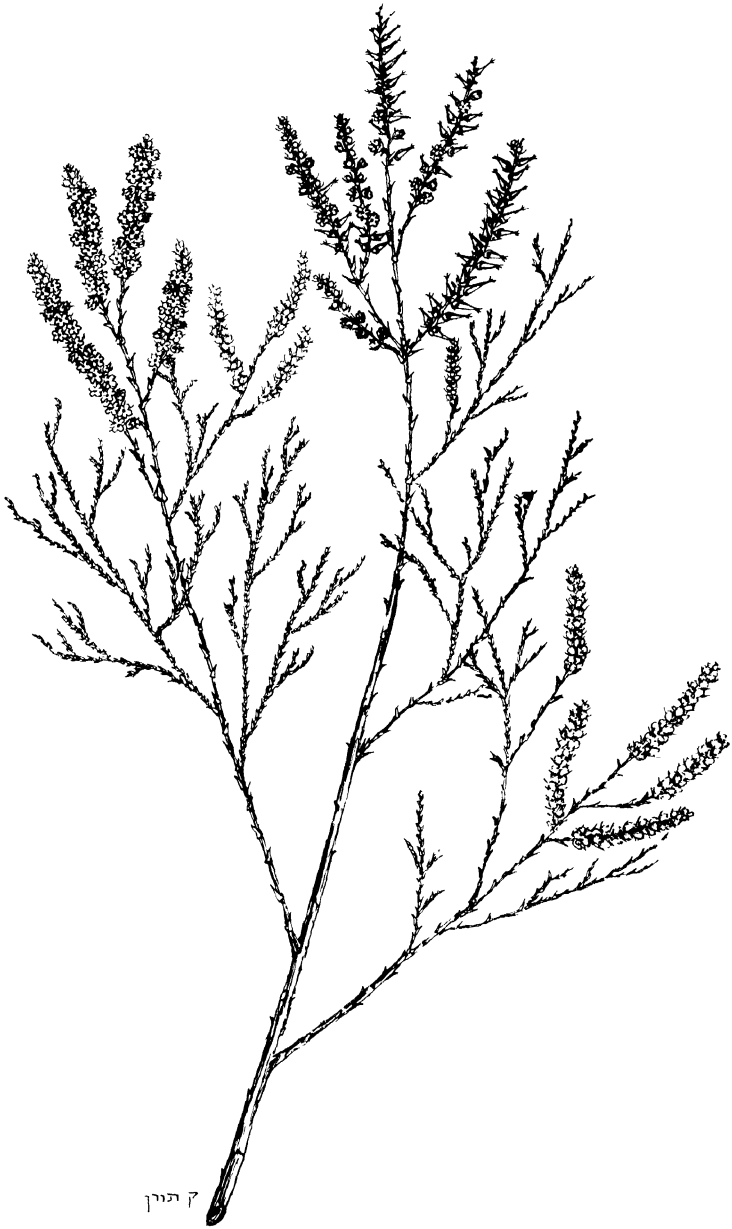


Fig. 62. *Tamarix gallica*.

Salsola tetrandra, Atriplex halimus, Prosopis farcta, Alhagi maurorum, Statice pruinosa, S. spicata, Bassia eriophora, Anthemis marismortui, and many other annuals. *Suaeda palaestina* is a succulent chamaephyte with a very shallow, much-branched root system never penetrating below a depth of 30 cm.

Of the fourth alliance, the SALSOLETUM TETRANDRAE deserves to be mentioned. The dominant *Salsola tetrandra* is a much-branching

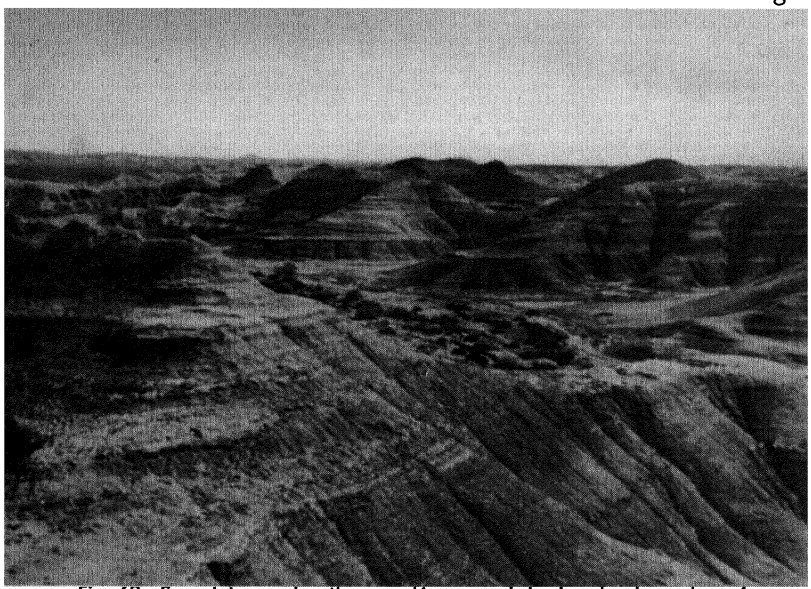


Fig. 63. *Suaedetum palaestinae* on Lissan marl, broken land, northern foreshore of the Dead Sea.

gray chamaephyte with small scalelike, succulent leaves. It has a shallow, spreading root system. It occurs associated with numerous annuals, such as *Stipa tortilis, Plantago ovata, Aizoon hispanicum, Mesembryanthemum nodiflorum, Reichardia tingitana, Aaronsohnia faktorovskyi, Reboudia pinnata, Erythrostictus palaestinus, Crepis arabica, C. obovata, Chlamydophora tridentata,* and many others.

The two last-mentioned alliances are marked by the high number of annual species they comprise. Many of them complete their life cycle within the very short period of the rainy season and are "desert wides" in the sense that the same species is found occurring in various associations of the two alliances. In contrast to them are the dominating chamaephytes that are exposed to drought and salinity. In dry years these chamaephytes are entirely leafless and the annuals are altogether lacking.

Generally the associations are arranged in belting systems, each belt corresponding to a definite range of salt concentration or duration of the inundation period. However, topographic disturbances and lateral ramifications of the salt water bodies often alter or efface the orderly arrangement of belts. An example of a more or less undisturbed zonal arrangement of the halophytic plant communities is found in the so-called "sebkha" of the southern Dead Sea foreshore. Here the following zonation has been noted: (1) a sterile belt subject to the tidal inundation of the sea, (2) a belt of *Arthrocnemum glaucum*, (3) a belt of *Arthrocnemum* mixed with *Tamarix gallica* var. *maris-mortui* and *T. deserti*, (4) *Tamarix deserti* and *Suaeda monoica* stands, and (5) *Nitraria retusa* (Fig. 64).

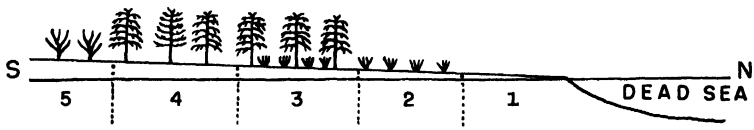


Fig. 64. Vegetation transect on the southern shore of the Dead Sea. 1, plantless, inundated foreshore; 2, belt of *Arthrocnemum glaucum*; 3, belt of *Arthrocnemum glaucum–Tamarix tetragyna* association; 4, belt of *Tamarix deserti* and *Suaeda monoica* stands; 5, belt of *Nitrarietum retusae*.

In the Arava Valley there are a series of smaller salines in which *Desmostachya bipinnata* and various species of *Tamarix* and *Nitraria retusa* form a zonational complex. Noteworthy are the eight species of *Tamarix* that grow in the salines of the Dead Sea and the Arava Valley, some of them endemic there.

For further details as to the ecology and distribution of the above communities the reader is referred to M. Zohary and Orshan (1949, 1956).

The Salicornietea Class. Some of the communities recorded in the salines of the Kishon and Na'aman area in the Acre Plain are discussed in the following.

SALICORNIETUM HERBACEAE is largely a pioneer community that occupies freshly emerged spots. The dominating *Salicornia herbacea* is often accompanied by *S. fruticosa*, *Cressa cretica*, *Pholiurus filiformis*, and *Hordeum marinum*. The amount of soluble salts in the soil decreases with depth and ranges from 2.8 to 3.5 per cent at a depth of from 0 to 20 cm. during summer, and the salt/water ratio averages 16 per cent.

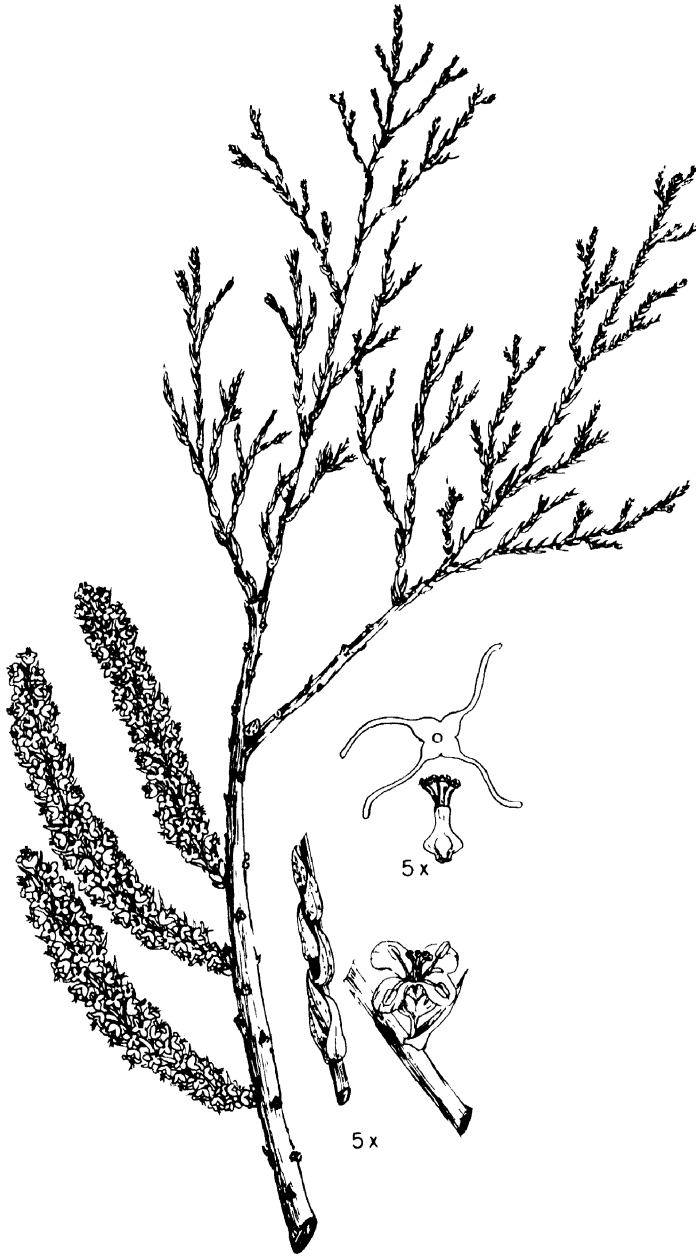


Fig. 65. *Tamarix meyeri.*

TAMARICETUM MEYERI MEDITERRANEUM occupies the banks of the Kishon and Na'aman rivers, as well as the borders of pools and puddles in their vicinity. *Tamarix meyeri* (Fig. 65) is often accompanied by *Arthrocnemum glaucum, Obione portulacoides, Juncus maritimus,* and *Salicornia* spp.

The *Arthrocnemum glaucum–Sphenopus divaricatus* association is the most common and characteristic community of the area. It occupies sites less flooded but more saline than the previously mentioned communities. Other leading species of more or less well-defined associations are *Statice limonium, Plantago crassifolia, Aeluropus repens,* etc. In open pools and puddles *Phragmites communis* and *Juncus maritimus* form almost pure stands. For further details on the coastal saline vegetation see Orshan and D. Zohary (1955).

8

Ecologic Behavior of Palestine Plants

Ecology of Dispersal

Botanists dealing with fruit and seed dispersal have grouped plants into anemochorous, hydrochorous, zoochorous, and autochorous according to the nature of their diaspores, their structure and appendages, or their mechanisms of discharge from the parent plant. There is a great deal of common sense in this classification, for no one denies the existence of a close correlation between the structure of the diaspore and the mode of dispersal. With regard to the adaptivity of diaspores to the agencies of dispersal, it is sufficient to mention the predominance of zoochorous plants in tropical and subtropical woods, of hydrochorous plants in littoral floras, and of anemochorous plants in alpine altitudes. The fact that morphologically different dispersal units (such as seeds, mericarps, fruits, and fruit aggregates) may simulate one another by their dispersal structures, shows that the dispersal apparatus is a highly adaptive character acquired through a long process of selection.

There are, however, a few drawbacks in this approach to the problem of dispersal. First of all, there are only a few studies based on observations and experiments formulated to obtain data on the functioning of the dispersal apparatus and the actual distances covered by the various types of diaspores, e.g., Dingler (1889), Small (1919), Hirsch (1901), Schneider (1935), and Hylander (1929). Second, there is only a very weak correlation between the perfection of the dispersal apparatus and the range of distribution of plants, as shown by De Candolle (1855). Examples can be provided from the Compositae, Salicaceae, Orchidaceae, and others, which abound in narrow endemisms despite their highly elaborate

anemochorous dispersal apparatus. Third, it has become routine to ascribe dispersal abilities to any appendages of seeds and fruits without examining their real function. Moreover, there are many types of "dispersal apparatus" which are not only unfit for long-distance dispersal but actually seem to hamper it, as will be shown later. And finally, the number of species with diaspores without any kind of equipment for long-distance dispersal is considerably higher than of those furnished with appendages or other accessories supposedly enabling long-distance transportation.

It is evident that wide-range dispersal, or telechory, is not the only means of dispersal in nature. There are many cases in which telechory is detrimental to survival of the species by its uncontrolled transportation of seeds into sites entirely unfit for the ecologic requirements of the species, and it is possible that many species have become extinct through total seed loss as a result of transportation into areas distant from the parental habitat.

A study of the dispersal behavior of the local flora (M. Zohary, 1937) has revealed that dispersal on the spot, or topochory, is not less common than telechory, and that in many cases appendages and enations of diaspores, conventionally interpreted as a means for long-distance dispersal, can be regarded as means of hindering transportation rather than favoring it. In the following paragraphs some features of topochory will be discussed at length, due to their prevalence and ecologic importance in arid floras.

Topochory. Topochory is achieved in a variety of ways. In many cases the diaspore is rendered unfit for transportation by its structure, its weight, or its accessories. In other cases, long-distance dispersal is forestalled by the particular way in which the diaspore is released from the parent plant or by the particular growth form of the latter. Examples of elaborate devices for the retention of the seeds within the vicinity of the parent plant are furnished by the long gynophores of geocarpic plants, the boring apparatus in many seeds and fruits, the anatomic structure peculiar to hygrochastic plants, etc. Considering such plants with regard to their environmental setting, one is led to the conclusion that under certain circumstances a restriction of the dispersal range favors the survival of species by ensuring suitable habitats to the progeny and by avoiding loss of seeds and fruits that may lead to the eventual extinction of the species. Topochory also has some bearing on the maintenance of populations by offering a chance of cross-pollination and by affecting germination behavior. The following ten types of topochory may be distinguished here (cf. also M. Zohary, 1937; Murbeck, 1919–20).

BARYSPERMY. This term signifies here the most common instances in which diaspores are heavy seeds unequipped for any mode of long-distance dispersal. The seeds fall from their containers near the parent plant. Even when the seeds are small, they are not blown away by the wind but adhere to the soil particles or enter pits and fissures of the dried-out soil surface. Examples are found in the Cruciferae, Cistaceae, Resedaceae, Primulaceae, Leguminosae, and other families.

CARPOSPERMY. There is a marked trend in the plant kingdom toward the production of diaspores which consist of monospermous fruits or mericarps. Many of such diaspores are lacking in special dispersal equipment. Examples of carpospermy are found in the Gramineae, Cruciferae, Leguminosae, Fumariaceae, Chenopodiaceae, Compositae, Umbelliferae, Malvaceae, Labiatae, and in many others. The formation of carpospermous diaspores in species both with superior and inferior ovaries indicates the universality of this trend in the evolution of diaspores within the seed-bearing plants. In most cases carpospermy has been achieved through degeneration of the separation tissues of the pericarp linked with the numerical reduction of the seeds per fruit. Another way of achieving carpospermy is schizocarpy, as in Malvales, Gruinales, Euphorbiaceae, Zygophyllaceae, Umbelliferae, Labiatae, Boraginaceae, and other families. Lomentation of polyspermous pods and siliques, such as is found in the Cruciferae, Leguminosae, Papaveraceae, etc., also results in the formation of one-seeded diaspores equipped with a pericarpial coating. In certain cases, for instance, in *Trifolium* and many Chenopodiaceae, carpospermous diaspores are fitted with additional perigonial coating or, in the case of *Artemisia,* certain species of *Centaurea* and others, with that of involucral origin. It is true that these extraseminal coatings offer more room for the development of appendages and protuberances than a delicate testa, but in many cases the latter hinder rather than aid long-distance dispersal because they increase the weight of the diaspores and bring about surface configurations that cause the diaspore to remain in the immediate vicinity.

SYNAPTOSPERMY. (Murbeck, 1919–20.) The feature in which two or more seeds or one-seeded fruits are joined to form a compound dispersal unit is called synaptospermy. It is very common throughout the plant kingdom, but it is largely restricted to arid regions. The Palestinian flora comprises 245 species with synaptospermous diaspores: they occur in a more or less equal percentage in Palestine's three plantgeographical territories and are found in various families

but are especially well represented in the Leguminosae, Cruciferae, Caryophyllaceae, and Gramineae.

The following genera of the local flora are particularly noteworthy for comprising one or more synaptospermous species: *Gymnocarpos, Paronychia, Pteranthus, Brassica, Enarthrocarpus, Erucaria, Ochtodium, Raphanus, Zilla, Astragalus, Coronilla, Hedypnois, Hymenocarpus, Onobrychis, Ornithopus, Prosopis, Scorpiurus, Trifolium, Trigonella, Malva, Statice, Arnebia, Ballota, Marrubium, Molucella, Phlomis, Salvia, Galium, Anthemis, Carduus, Catananche, Centaurea, Xanthium, Aegilops, Agropyron, Avena, Boissiera, Cornucopiae, Cynosurus, Elymus, Heteranthelium, Lagurus, Lepturus, Monerma, Pennisetum, Psilurus, Triticum,* and many others.

Of the numerous morphologic-ecologic types that have been distinguished among synaptospermous diaspores, only a few are mentioned here. In some species of *Trifolium* entire fruit heads, each containing scores of seeds, are detached from the plant and form a single dispersal unit. These units persist until after germination. In *Astragalus* and other leguminous plants, many-seeded, indehiscent pods or groups of one-seeded pods form dispersal units. In some Cruciferae the diaspores are composed of indehiscent stylar parts or of entire pods or loments. In many grasses the dispersal unit consists of entire spikes or compact, headlike panicles. In some Labiatae and Boraginaceae the unit consists of the four mericarps enclosed in the persistent calyx. In most of these cases the diaspores are comparatively heavy. They are often devoid of a special apparatus for long-distance dispersal or are so shaped that they are not readily transported by the prevailing dispersing agents. Very often one encounters these units close to parental plants several months after dissemination.

An interesting group is that of the "tumbleweeds," in which entire seed-bearing shoots break at seed maturity near the base of the stem and are carried by the wind. They are members of the genera *Salsola, Vaccaria, Leontice, Cachrys, Phlomis, Salvia, Teucrium, Centaurea, Cousinia, Gundelia, Allium, Bellevalia, Muscari,* and others. Almost all belong to the Irano-Turanian element.

Synaptospermy is derived in most cases from monospermy. It is no doubt an advanced evolutionary stage associated with the degeneration of separation tissues in pods, legumes, loments, and capsules, with the formation of abscission tissue in joints of peduncles and pedicels, and with a series of other characteristics. In fact, the synaptospermous species are found in genera belonging to phylogenetically advanced groups within their respective families, such as Brassicinae, Galegeae, Hordeae, Paronychieae, and others.

MYXOSPERMY. Seeds or one-seeded fruits of many species, when moistened, exude mucilage from their testal or pericarpial layers. When released from their containers in early spring, such seeds are often moistened by late rains and, by virtue of this mucilage, adhere to the soil surface until the beginning of the following rainy season. Myxospermy is fairly common in the Cruciferae, Labiatae, Compositae, Plantaginaceae, and in other families.

TRYPANOCARPY. In some species the one- or few-seeded diaspore is equipped with a hygroscopic drilling apparatus or with a sharply pointed tip, which enables it to penetrate the soil. Observation has shown that such boring units are quite unable to traverse distances and that their movement is arrested by fissures or other minor obstacles on the soil surface. Examples of trypanocarpy occur in the genera *Erodium, Chardinia, Aegilops, Andropogon, Aristida, Bromus, Elymus, Geropogon, Hordeum, Stipa, Triticum,* etc.

HYGROCHASY. In hygrochastic plants, seeds or one-seeded fruits are not released from their containers until the latter or their carriers have been moistened or drenched by water. Movements are effected by a shrinking and swelling mechanism (Steinbrinck, 1906, 1925; von Guttenberg, 1926; Fahn, 1947; M. Zohary and Fahn, 1941). The restrictive effect of hygrochasy upon long-distance dispersal is reflected in the following. Dissemination does not take place immediately after the fruit has ripened but is delayed for a considerable period until the beginning of the rains. After the first few days of rain the seeds or fruits are released from their containers and begin to germinate immediately and so possibilities of further dispersal are forestalled. There are over 40 species of hygrochastic plants in Palestine's flora, e.g., *Anastatica hierochuntica, Notoceras bicorne, Salvia horminum, Cichorium pumilum, Asteriscus pygmaeus,* etc.

BASICARPY. This occurs in a series of stemless annuals whose compact inflorescences are borne close to the soil surface and whose fruits or fruit aggregates remain attached to the dead plant in general. Germination occurs on the spot and often within the seed containers. Examples of basicarpic species are *Astragalus tribuloides, Trifolium tomentosum* (particular form), *Trigonella stellata, Plantago cretica, Evax contracta, E. palaestina, Filago prostrata, Gymnarrhena micrantha, Rhizocephalus orientalis, Ammochloa acaulis,* and others.

HETEROCARPY. In this type the individual plant produces two kinds of diaspores, one of which is generally telechorous, while the other is topochorous. Among the 100 or so heterocarpic species of the local flora several types have been distinguished according to the morphologic peculiarities of their diaspores. In many Compos-

itae the outer achenes of the flower head differ from the inner ones in size and form, as well as in the degree of the pappus development. In some Umbelliferae, mericarps of the same umbel may differ from each other in shape, surface configuration, and size. In some heterocarpic Cruciferae the valvar part of the siliqua opens and discharges the seeds, while the stylar seed-bearing part is indehiscent. In many species of the genus *Aethionema* two types of silicules are produced: indehiscent one-seeded and dehiscent many-seeded ones. In the Gramineae (*Phalaris, Aegilops,* etc.), dispersal units on an individual ear may vary from each other in shape and development of awns. It has been shown that the two kinds of disseminules also differ from one another in the time of their detachment from the parent plant and, partly at least, in their suitability for long-distance dispersal. Most striking is the difference in time of germination between the different types of dispersal units. In some Compositae, for example, it has been shown that there is a marked delay in the germination of marginal achenes as against the central ones, particularly in cases where the former are enclosed in involucral bracts. Even more pronounced is the delay when the seed is enclosed in the pericarp, e.g., various hetero-mericarpic Cruciferae. The reason for the retardment can be the presence of an inhibitor substance in the pericarpial or involucral tissue (M. Zohary, 1937; Sroelov, 1940; Evenari, 1949).

Heterocarpy is characteristic of semiarid and arid floras. It occurs in various families but is most common in the Compositae (especially the Liguliflorae), Umbelliferae (e.g., Daucinae), Cruciferae (e.g., Brassicinae), and Gramineae (e.g., Hordeae).

AMPHICARPY. Amphicarpy is the phenomenon in which a plant produces aerial as well as subterranean fruits so that a portion of the seeds are retained in the close vicinity of the parent plant. In Palestine, amphicarpy has been found in *Emex spinosus, Pisum fulvum, Vicia angustifolia, Catananche lutea,* and *Gymnarrhena micrantha.* In all of these, differences between the aerial and subterranean flowers and fruits are fairly pronounced.

GEOCARPY. In geocarpic plants all the fruits of the individual are produced beneath the soil surface and remain there until germination. A distinction may be made between protogeocarpy, in which both the flowers and the fruit are subterranean (e.g., *Biarum* spp.) and hysterogeocarpy, in which the fertilized ovary penetrates into the soil by means of a long gynophore or peduncle. The fruits then ripen in the soil. Examples are *Faktorovskya aschersoniana, Trifolium subterraneum,* and *Callitriche pedunculata.* Geocarpy has

been studied in detail by various authors (Theune, 1917; Schmucker, 1923; M. Zohary and Orshan, 1947a; M. Zohary, 1937; and others). It is the most extreme way of keeping seeds in the close vicinity of the parent plant.

In all of the above types, long-distance dispersal is largely or entirely impeded. Such adaptations can be related to arid and semi-arid regions on the assumption that in areas where plant life is confined to small niches surrounded by abiotic deserts, dispersal of seed outside the favorable habitat is likely to be fatal to the survival of the species.

The predominance of telechory in woodland communities on one hand and that of topochory in plant communities of open desert vegetation on the other is illustrated by the following two sample records. The first is taken in the Mediterranean association of *Quercus calliprinos* in upper Galilee, and the second is taken in the Saharo-Sindian ZYGOPHYLLETUM DUMOSI of the central Negev. The method of seed dispersal in each case is indicated by capital letters, as follows: A = anemochory, Am = amphicarpy, Au = autochory, B = basicarpy, Ba = baryspermy, C = carpospermy, G = geocarpy, H = heterocarpy, Hy = hygrochasy, M = myxospermy, S = synaptospermy, T = trypanocarpy, Z = zoochory.

QUERCUS CALLIPRINOS–PISTACIA PALAESTINA Association

Dryopteris villarsii	A	*Cyclamen persicum*	Z
Clematis flammula	A	*Pancratium parviflorum*	Z
Ophrys fusca	A	*Poterium spinosum*	S
O. bornmuelleri	A	*Andropogon distachyus*	T
Cephalanthera longifolia	A	*Stipa aristella*	T
Anacamptis pyramidalis	A	*Quercus calliprinos*	Z
Orchis anatolicus	A	*Pistacia palaestina*	Z
O. papilionaceus	A	*Crataegus azarolus*	Z
O. galilaeus	A	*Arbutus andrachne*	Z
Dactylis glomerata	A	*Rhamnus alaternus*	Z
Bromus tomentellus	A	*R. palaestina*	Z
Crepis hierosolymitana	A	*Phillyrea media*	Z
Ranunculus asiaticus	A	*Osyris alba*	Z
Atractylis comosa	A	*Ruscus aculeatus*	Z
Melica minuta	A	*Smilax aspera*	Z
Trifolium erubescens	A	*Bryonia syriaca*	Z
Spartium junceum	Au	*Arum palaestinum*	Z
Calycotome villosa	Au	*Amygdalus communis*	Z
Lotus judaicus	Au	*Styrax officinalis*	Z
Thrincia tuberosa	H	*Laurus nobilis*	Z
Crepis palaestina	H	*Asparagus aphyllus*	Z
Cistus salvifolius	Ba	*Rubia olivieri*	Z
Carex distans	Ba	*Tamus communis*	Z
Hypericum serpyllifolium	Ba	*Lonicera etrusca*	Z
Oryzopsis miliacea	Ba		

ZYGOPHYLLETUM DUMOSI

Zygophyllum dumosum	A	*Helianthemum salicifolium*	Ba
Reaumuria palaestina	A	*H. kahiricum*	Ba
Anabasis articulata	A	*H. ledifolium*	Ba
Atractylis serratuloides	A	*Allium modestum*	Ba
Scabiosa aucheri	A	*Diplotaxis harra*	Ba
Silene setacea	A	*Linaria haelava*	Ba
Herniaria hemistemon	B	*Notoceras bicorne*	Hy
Asteriscus pygmaeus	B, Hy	*Plantago coronopus*	Hy
Gymnarrhena micrantha	B, H, Am	*Carrichtera annua*	Hy
Filago prostrata	B	*Plantago ovata*	M
Trigonella stellata	B	*Gymnocarpos fruticosum*	S
Erucaria boveana	H	*Reboudia pinnata*	S
Aaronsohnia faktorovskyi	H	*Medicago laciniata*	S
Reichardia tingitana	H	*Aegilops kotschyi*	S
Senecio coronopifolius	H	*Astragalus callichrous*	S
Centaurea aegyptiaca	H	*A. tribuloides*	S, B
C. hyalolepis	H	*Pteranthus dichotomus*	S
Calendula aegyptiaca	H	*Paronychia sinaica*	S
Picris damascena	H	*Arnebia decumbens*	S
P. intermedia	H	*Stipa tortilis*	T
Spergularia diandra	Ba	*Bromus fasciculatus*	T

The proportions between the above-listed telechorous and topochorous plants in mesic and in arid habitats may be summed up as follows.

MEDITERRANEAN MAQUIS		SAHARO-SINDIAN HAMMADA VEGETATION	
Zoochory	42 %	Zoochory	0 %
Anemochory	40 %	Anemochory	14.5 %
Total telechory	82 %	Total telechory	14.5 %
Baryspermy	8 %	Baryspermy	16.5 %
Trypanocarpy	4 %	Trypanocarpy	5 %
Heterocarpy	4 %	Heterocarpy	21.5 %
Synaptospermy	2 %	Synaptospermy	19 %
Total topochory	18 %	Basicarpy	14 %
		Myxospermy	2.5 %
		Hygrochasy	7 %
		Total topochory	85.5 %

Germination Ecology

The following paragraphs will contain a discussion of the timing of germination and its ecologic significance. In regions where the year is divided into a rainy and a dry season, germination out of the proper season may result in the desiccation and dying off of large numbers of seedlings. This endangers the very survival of species by fruitless wastage of the seed reserves in nature. One may thus look on the following factors as means that keep germination in nature

within that season which is likely to secure the development of the seedling and the completion of the plant's life cycle.

1. Exogenous factors: temperature, moisture, etc.
2. Endogenous factors: dormancy in its strict sense, i.e., late structural and biochemical maturing of the embryo or endosperm or both; inhibition of germination through the presence of chemical substances in the seeds or their coats; impermeability of the seed coat or the endosperm to moisture and gases; uneven distribution of germination within the season; and retardment of dispersal.

A few examples taken from the local flora demonstrate the working of these two series of factors in controlling germination periodicity.

Exogenous Factors. In both the Mediterranean and desert parts of Palestine, germination is more or less exclusively limited to late autumn (November–December) and spring (March–April). Climatic fluctuations from year to year may cause an earlier or later onset of germination. The majority of the native flora germinates in autumn and only some boreal and tropical weeds or aquatics in spring, e.g., species of *Amaranthus, Atriplex, Portulaca, Sonchus, Panicum, Echinochloa, Cyperus,* etc. Only a few winter annuals with early fruit setting, such as *Diplotaxis erucoides, Calendula aegyptiaca, Erucaria boveana, Plantago psyllium,* and others may form two generations during their growth period. The same is true for some summer annuals, such as *Sonchus oleraceus, Erigeron crispus,* and *Amaranthus* spp.

Of the climatic factors controlling germination periodicity in the winter flora, moisture in the form of rain is the most important. Germination commences suddenly with the advent of the first rains, which break the six-month drought. That availability of moisture alone determines the time of germination in winter plants is shown by the fact that many are able to germinate in other seasons of the year when supplied with sufficient moisture; examples are *Erucaria boveana, Reboudia pinnata, Eremobium lineare, Carrichtera annua, Hippocrepis bicontorta, Ononis reclinata, Cephalaria syriaca, Pallenis spinosa, Aegilops longissima, Bromus fasciculatus,* and *Lolium temulentum.*

The number of plants in which the timing of germination in nature is controlled by temperature plus moisture is probably considerable, although only few species have been investigated in this respect. In some species the seeds are able to germinate only after they have been exposed for a certain length of time to low temperatures (mostly between 5 and 10° C.). To this group belong, for instance, *Sinapis*

arvensis, Hirschfeldia incana, Savignya aegyptiaca, and *Tetragonolobus palaestinus.* In other cases the ability to germinate depends on an exposure to high temperatures for a shorter or longer period. In nature the resting seeds of many plants are affected by low temperatures in autumn and/or by high temperatures in summer. On the whole, one can conclude that the periodicity of germination, a feature vital to species survival, is in natural habitats largely conditioned by seasonal changes of the climate.

Endogenous Factors. The structure of the diaspore and the biochemical processes involved in the completion of seed maturation prevent untimely germination in numerous species of the local flora. This delay is especially important for those species whose fruits ripen before the last winter rains, when sufficient moisture is still available for germination but not for the complete development of the life cycle. In most species of this category the delay does not exceed a period of two to three months; in others, however, this type of seed dormancy lasts for six months or more.

The delaying influence which the seed coat may have on germination is well known and need not be emphasized. It is noteworthy that a large percentage of the local flora belongs to that group whose germination is controlled by the impermeability of the seed to water and gases, which is caused both by hard testas and by pericarpial and/or perigonial envelopes. In carpospermy, synaptospermy, and heterocarpy—features so common in the local flora—extraseminal coating may be looked upon as a major factor causing considerable delay in germination. In many cases substances inhibiting germination also occur in these coats, as has been shown by Evenari (1949) and others. Care must be taken here to distinguish the mechanical from the chemical effect.

Unequal timing of germination of seeds in one and the same species or individual is another common feature exhibited by many plants. Some germinate early in the season, others later, and others not before the following year. Some examples are species of *Medicago, Astragalus, Trigonella, Onobrychis, Hymenocarpus, Aegilops, Neurada,* and *Pteranthus.* This is particularly noteworthy in *Onobrychis squarrosa.* Only the upper seed of the two in the indehiscent legume germinates, as a rule, in the first year, while germination of the second seed is delayed till the following year (M. Zohary, 1937).

An effjcient device for periodical spreading of germination is found in heterocarpous and heteromericarpous plants (see preceding paragraph). In some species of Brassicinae the seeds included in the stylar indehiscent part of the pod germinate considerably later than

those released from the dehiscent valvar part. In most of the cases examined the reason for this delay has been shown to be the presence of inhibiting substances in the stylar part (M. Zohary, 1937; Sroelov, 1940). Examples of this group are *Sinapis arvensis*, S. *alba*, *Hirschfeldia incana*, *Brassica tournefortii*, and *Erucaria* spp. The same seems to be true of the marginal achenes in the Compositae, as exemplified by *Hedypnois cretica*, *Hyoseris glabra*, *Rhagadiolus stellatus*, various species of *Crepis*, *Garrhadiolus*, and many others.

Delay of dispersal is another factor preventing premature germination. Hygrochastic plants, whose seed receptacles open only after they have been sufficiently moistened, retain their seeds during the dry season and release them only after the first rains. Sometimes not all the seeds are released at the same time, e.g., in *Asteriscus* some of the achenes are retained within their receptacles throughout the subsequent year.

In yet another group of plants fruit-setting does not occur before late autumn. Examples are species of *Anabasis*, *Haloxylon*, *Salsola*, *Artemisia*, *Quercus*, and others. Germination in these plants occurs as soon as seeds have been discharged, with the first rains.

All these factors and devices, highly important as time regulators of germination, are without doubt the result of adaptation of floras to climatic conditions by means of natural selection. Retardment and spreading of germination over a long period are closely connected to higher seed viability, which is a feature of vital ecologic importance in the survival of annual species, especially in arid regions. The fact that large quantities of seeds are being preserved over a number of years in arid parts of Palestine is evident from the occasional mass reappearance of many annual species after consecutive years of drought during which they are entirely absent.

Morphoecology

Some morphologic and anatomic features connected with plant behavior, especially in respect to water economy, will now be discussed.

Root Habits (Fig. 66). Root morphology and ecology have been studied by various authors (Cannon, 1925; Weaver, 1919; and many others). The following paragraphs review the root habits of some local plants in the light of plant-water relations. Only perennial plants, which are exposed to summer drought, are considered here. The dimensions, branching, and orientation of their root system are discussed below.

1. Within a given habitat plants with various root forms may occur. To record a single instance only, in the deep saline soils of

the Dead Sea region, side by side with the shallowly rooting *Suaeda palaestina* and *Salsola tetrandra,* one finds extremely deep-rooting plants such as *Prosopis farcta, Alhagi maurorum,* and *Suaeda monoica* (Fig. 67).

2. Although plants with deep root systems are generally unable to adapt themselves to shallow soils, surface-rooters can increase their root length considerably in deep soils, provided moisture conditions improve with depth. For instance, the shallow-rooting *Zygophyllum dumosum* and *Haloxylon articulatum* have longer roots when growing on wadi banks.

3. Allorhizous root systems with horizontal as well as vertical laterals are typical of trees and high shrubs, especially in maquis and forests. The proportion between these two types of laterals is largely conditioned by soil constitution. Such root systems are most flexible and adaptable to rocky ground, where generally most of the laterals spread near the surface, while only a few penetrate into the rock crevices or deep-seated soil pouches.

4. In desert plants the roots are mostly confined to the upper soil layers because the rain does not penetrate into the deeper ones.

Of the main root forms so far distinguished in the local perennials, the following may be mentioned:

THE OLEA TYPE (Fig. 66A, B). The root system forks near the thick crown and some of the laterals expand horizontally in the top soil layer, while the remainder grow downward. The proportion between these two kinds of branches varies largely with the depth of the subsoil layer. Where it is very rocky, the majority of laterals remain near the surface and only a few penetrate fissures and crevices. In deep soil the contrary has been observed. This type is predominant in the maquis trees and shrubs on the rocky slopes of the Mediterranean mountain range. During summer, when the surface layers of the soil are deficient in moisture, the water balance of the plants is maintained mainly by the vertical roots. Water intake and plant growth are thus largely dependent on the proportion of such growing roots. Accordingly, one may find very considerable differences in the water output by transpiration and in the development between two neighboring individuals of the same species. In some instances, vertical roots have been uncovered to a depth of 4 m. without reaching their extremities.

THE DESMOSTACHYA TYPE (Fig. 66C). The rootstock of this plant grows vertically to some depth before giving off very long horizontal laterals. Vertical offshoots from the latter descend further and branch horizontally again, etc. The dimensions of the subterranean

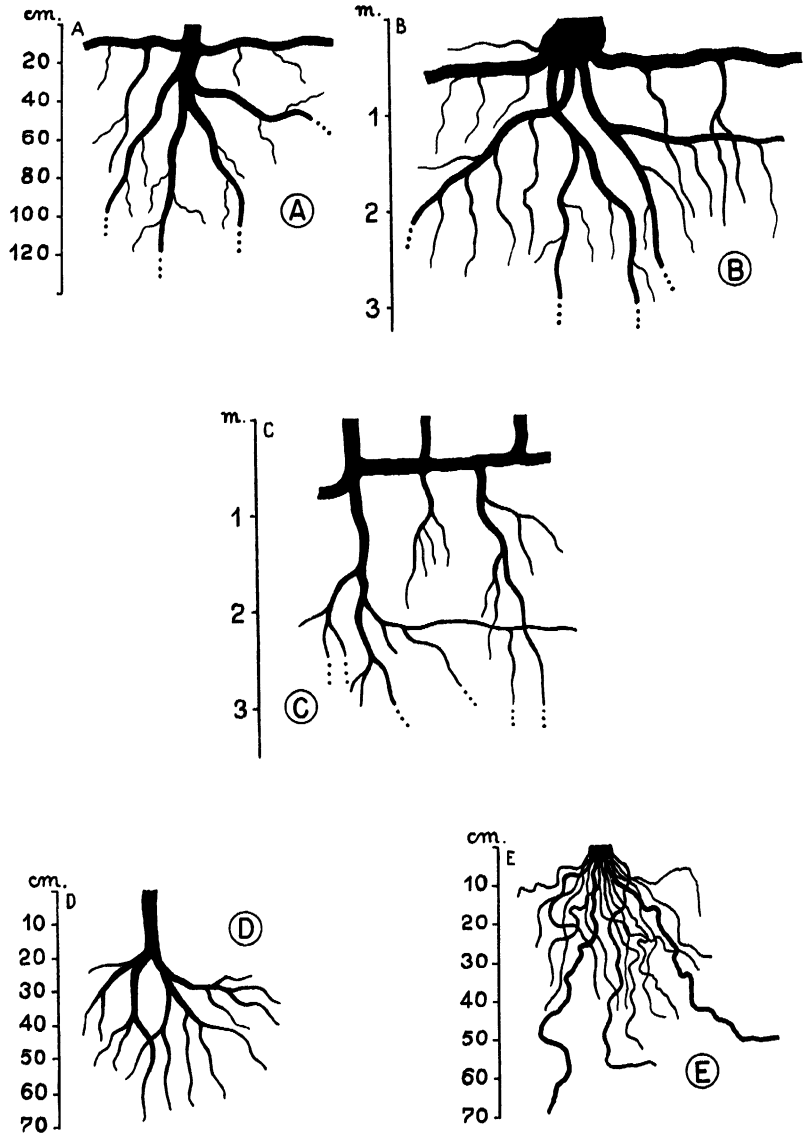


Fig. 66. Root types. A, B, forms of the *Olea* type; C, *Desmostachya* type; D, E, forms of the *Poterium* type; F, G, forms of the *Tamarix* type; H, *Suaeda* type.

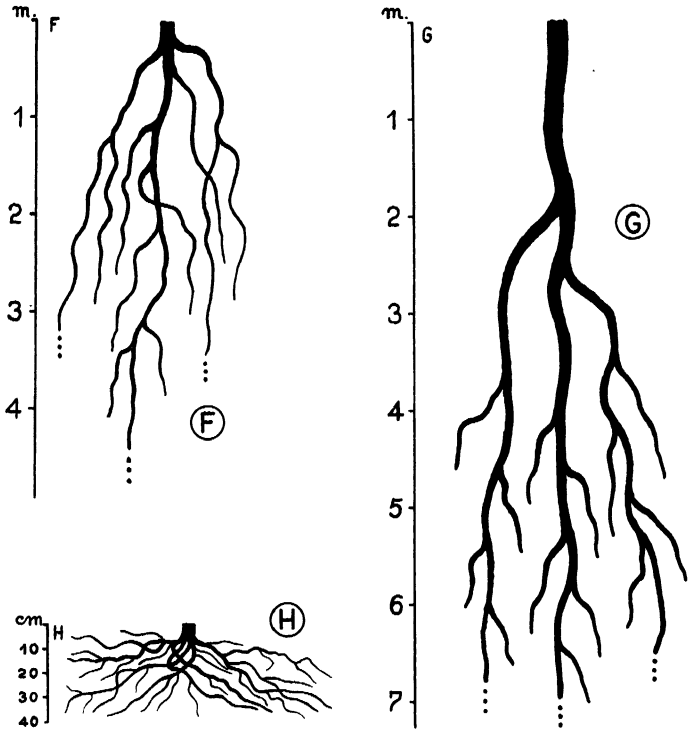


Fig. 66 *(Cont.)*.

shoots and roots of this plant are so enormous that a single individual may occupy an acre plot, with hundreds of aerial shoots sprouting from the rootstock. A similar pattern of subterranean rootstock ramifications has been observed in *Prosopis farcta,* which is the predominant weed of alluvial soils. This system has been followed up to a depth of 15 m. and this was still nowhere near its end. Here, too, scores of aerial "bushes" may issue from a single rootstock. *Acacia albida* and *Alhagi maurorum* can also be included in the same type.

THE POTERIUM TYPE (Fig. 66D, E). The root system is generally made up of a main vertical taproot, many branched and with diagonal laterals. Sometimes all main lateral branches occur near the crown, where they form a somewhat fibrous system. Depth is generally limited between 0.5 and 1 m. Adaptability of this root system to the nature of the subsoil is manifested by its flexibility both in branching and orientation of the laterals. This type is common to

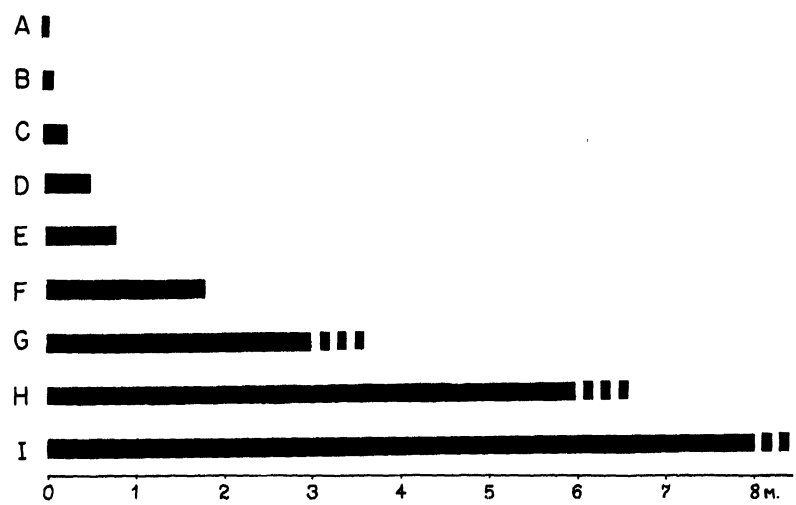


Fig. 67. Root lengths of different species growing in the same *Suaedetum palaestinae* association in the Dead Sea salines. A, *Mesembryanthemum nodiflorum;* B, *Sphenopus divaricatus;* C, *Phalaris minor;* D, *Suaeda palaestina;* E, *Salsola vermiculata;* F, *Statice pruinosa;* G, *Atriplex halimus;* H, *Alhagi maurorum;* I, *Prosopis farcta.*

most of the local batha and garigue plants in the Mediterranean territory.

THE TAMARIX TYPE (Fig. 66F, G). The vertical roots of this type are the longest and deepest observed in this area, and often reach the water table. Given enough space, laterals of a considerable length may also develop. Both the verticals and laterals are poorly branched. Examples are *Tamarix* spp., *Retama raetam, Atriplex halimus,* and *Acacia raddiana.*

THE SUAEDA TYPE (Fig. 66H). The root system is generally very shallow and reaches a depth of 50 cm. only in exceptional cases; in width, however, it may attain a diameter of 1 m. or more. The system is many branched, the main taproot being undeveloped. The laterals are concentrated near the root crown and spread out horizontally. This is the most common form in local desert shrubs on the hammada and dry saline soils in which available moisture or low salinity, or both, are confined to upper layers. This system has been observed in *Suaeda palaestina, S. asphaltica, Atriplex parvifolia, Salsola tetrandra, Zygophyllum dumosum, Reaumuria palaestina,* and others.

THE PINUS TYPE. Here the bulk of the root system consists of shallow, much-branched, horizontal roots that form a superficial disc-like fibrous body from which only few thin vertical roots descend and penetrate rock fissures and solid soft rocks. These vertical root threads have few, weakly developed laterals, which cannot secure the tree against windfall.

THE ARTEMISIA TYPE. Here the root system consists of more or less fibrous, vertical branches, 10–30 cm. long. So far it has only been observed in *Artemisia herba-alba,* when growing on hills with a very shallow soil layer. In deeper soils the roots are considerably longer.

THE VERBASCUM TYPE. The vertical, relatively thick and very poorly branched taproot reaches a depth of 1–2 m. This type is characteristic of most hemicryptophytes with two growth seasons. Examples are *Ononis leiosperma,* species of *Verbascum, Onopordon,* and *Echinops.*

Seasonal Changes in the Plant Body. In a flora subjected to seasonal fluctuations of water supply, changes that are of utmost hydroecologic importance occur in the plant body throughout the year. The timing and extent of these changes in the local flora will now be reviewed.

1. Over 50 per cent of Palestine's plants are annuals. The majority of them are winter annuals, which complete their life cycles in spring (April–May) or earlier. A small proportion are summer annuals, mostly weeds or ruderals of boreal or tropical origin which start their development in spring or early summer. There are only very few biseasonal annuals, such as *Salsola inermis* and *Euphorbia aleppica,* that drop their main stem leaves at the end of the rainy season and continue their physiologic activity by means of upper leaves accompanying the flowering shoots.

2. Geophytes resemble annuals in that their aerial shoots die at the end of the rainy season. There are, however, a few geophytes that flower in late summer when the drought is at its maximum, e.g., *Biarum* spp., *Urginea* spp., and *Pancratium* spp. In these geophytes the leaves appear after flowering and are developed mainly in the rainy season. The reason for this early flowering, which is disharmonious with climatic conditions, is unknown.

3. On the basis of their behavior, perennial herbs can be grouped as follows. (a) Winter perennials whose entire aerial shoots die away after flowering in spring or early summer. This group comprises most of the hemicryptophytes, e.g., *Paronychia* spp., *Psoralea bituminosa, Ferula* spp., *Convolvulus* spp., perennial grasses, and

others. (b) Summer perennials whose aerial shoots begin developing sometime during summer and disappear at the end of the dry season. Examples are *Capparis* spp., and *Prosopis farcta.* (c) Biseasonal perennials which develop their vegetative leafy shoots or leaf rosettes in winter and their flowering shoots during summer. These latter are often green and bear small leaves, enabling the plants to be physiologically active throughout the year. Examples are *Polygonum* spp., *Verbascum* spp., *Cirsium* spp., *Carlina involucrata, Tolpis virgata,* and *Echinops* spp.

4. Among the shrubs and trees the following types can be distinguished. (a) Summer deciduous shrubs, such as *Anagyris foetida, Euphorbia thamnoides,* and *Lycium* spp. (b) Winter deciduous trees, of which examples are *Quercus ithaburensis, Crataegus azarolus,* and *Styrax officinalis.* (c) Biseasonal shrubs and trees, of which three further subtypes can be distinguished: true evergreens, such as *Laurus nobilis, Myrtus communis,* and *Arbutus andrachne,* which retain their shoots and leaves unreduced all the year round; heterophyllous evergreens, which replace the larger winter leaves by small or scalelike summer leaves, such as *Poterium spinosum, Salvia triloba,* and *Thymus capitatus;* and spartoid evergreens, which shed their leaves at the end of the rainy season but remain physiologically active by means of their green shoots, e.g., *Ochradenus baccatus, Retama raetam,* and *Spartium junceum.*

According to the morphologic changes that occur in the plant body during the year the following groups can be distinguished in the local flora (Orshan, 1953).

Plants in which either the whole plant body or the whole aerial shoot dies off each year at a definite season (annuals and many perennials).

Plants in which the upper parts of branches die off and are shed (*Ephedra* spp., *Calligonum comosum, Tamarix* spp., and others).

Plants in which the tips of older branches die off and the winter leaves are shed at the beginning of the dry season (*Retama*).

Plants in which the flowering branches die away after flowering and the winter leaves are replaced by smaller summer ones (most of the chamaephytes).

Plants in which the new leaves appear each spring before the older ones are shed (evergreens).

Plants in which the winter leaves disappear from the lower part of the shoot, while the smaller leaves of the flowering branches persist during summer (e.g., *Foeniculum* spp., *Artemisia herba-alba, Varthemia iphionoides,* and many others).

Leaf-shedding plants. Summer shedders: *Anagyris foetida, Lycium* spp.; winter shedders: *Quercus* spp., *Pistacia* spp., *Styrax officinalis,* etc.

Plants shedding their leaflets but retaining their green petioles, e.g., *Zygophyllum dumosum.*

Bark-splitting plants. The shoots of the articulate succulents, such as *Anabasis* spp., *Haloxylon* spp., and others, are covered with a succulent green assimilatory "coat" that dries out, splits, and is shed from the shoots after one or two years.

Cambial Activity. The seasonal rhythm of cambial activity in local Mediterranean trees has been studied by Fahn (1953, 1958). It begins at the end of March in all trees investigated, both deciduous and evergreen, except in *Ceratonia siliqua,* in which it commences in April. There is, however, a marked difference between evergreen and deciduous trees with regard to the time of bud-break. In deciduous types it starts in February and March, and in evergreens in April. The duration of cambial activity varies with the species, regardless of their being deciduous or evergreen. The shortest duration of cambial activity, lasting from March to July, has been recorded in *Crataegus azarolus,* while the longest, from April to the following March, was found in *Ceratonia siliqua.* Cambial activity in other species ceases between August and October. All trees under review produce annual rings of spring, summer, and late summer wood in proportions varying with the species. The smallest proportion of summer wood is produced by *Crataegus* and the largest by *Pistacia atlantica.*

Seasonal cambial activity appears to be dependent on the prevailing climatic rhythm, but it is the decrease in water supply in summer rather than temperature that causes its cessation. As to *Ceratonia siliqua,* its flowering time and distribution suggest its tropical origin and its alien behavior in cambial activity may serve as additional evidence for this suggestion.

Heat Resistance

Resistance to high temperatures in local maquis trees and shrubs was studied by Konis (1949), using the slightly modified method of Rouschal (1938b) and Clum (1926). Konis observed that the highest temperatures that leaves withstand under natural conditions are considerably lower than those found to be lethal under experimental conditions, as shown in Table 4. It has further been shown that lethal temperatures are lower for younger than for fully developed

leaves and that deciduous plants are less heat-resistant than evergreens. From these data it can be concluded that heat in itself is far from being a damaging factor in maquis plants under natural conditions.

TABLE 4

Maximal Temperatures of Leaves of Some Maquis Plants (Konis, 1949)

Plant	Highest Leaf Temperature Observed Under Natural Conditions * (° C.)	Lowest Experimental Temperature Producing Lethal Effects (°C.)
Rhamnus alaternus L.	52.5	59
Arbutus andrachne L.	49.6	53 (young leaves)
Laurus nobilis L.	49.5	56
Rhamnus palaestina Boiss.	47.6	53
Ceratonia siliqua L.	47.2	50.5 (young leaves)
Quercus calliprinos Webb	47.0	59
Phillyrea media L.	46.5	58
Cercis siliquastrum L.	45.8	56
Pistacia palaestina Boiss.	44.8	57

* Measured by thermocouple.

Water Relations

The problem of water balance in plants growing under arid and subarid conditions has interested many ecologists, but the published data in this field are too scattered and lack a general comparable base. It is the author's belief that Palestine, with its diversity of ecologic conditions, is an appropriate source for supplying such comparable data, notably because they were collected in various natural plant communities and obtained through a uniform method of research.

Transpiration. Investigations into the hydroecology of local plants, started by Oppenheimer (1932) on cultivated trees and shrubs, were first carried out on desert plants by Evenari (Schwarz) and Richter (1937). In 1948 Shmueli published transpiration data on local halophytes, and M. Zohary and Orshan (1954, 1956) on various desert plant communities. Most of the data quoted below are based on monthly or periodic measurements of the leading plants of various communities. The method used was that of rapid weighing, using a torsion balance (Huber, 1927).*

* Criticism has recently been voiced regarding the use of this method, especially with regard to readings taken from detached plant organs (Weinmann and Le Roux, 1946, and others). In defense of this method, which is widely used by ecologists, it

The amount of water lost by transpiration was related to the fresh weight or water content of the transpiring organ, and expressed in mg. of water lost by 1 g. of fresh weight of the transpiring organ per 1 min. (mg./g.min.) or 1 hour (mg./g.h.). In other readings the amount of water lost by transpiration was referred to the surface area of the transpiring organ (mg./dm.min.).

The following recordings are for selected summer days or for summer and winter days. The figures are mg./g.h., the Roman numerals in brackets indicating the month in which the reading was taken.

HYDROPHYTES, HULEH SWAMP. M. Zohary and Konis, 1944 MS.: *Cyperus papyrus* 522 (III)–966 (IX); *Dryopteris thelypteris* 1146 (IX); *Lythrum salicaria* 1182 (III)–2130 (IX); *Cynanchum acutum* 2268 (IX); *Typha angustata* 1208 (III)–2504 (IX); *Polygonum acuminatum* 1326 (III)–1344 (IX); *Lycopus europaeus* 3084 (IX).

SEGETAL PLANTS, MIQVEH ISRAEL (M), JERUSALEM (J). A. Abraham, 1949 MS.: *Carthamus tenuis* (J) 1330 (V)–1128 (VIII); *Prosopis farcta* (M) 1780 (V)–1962 (IX); *Convolvulus hirsutus* (J) 1870 (V)–1608 (VIII); *Ononis leiosperma* (J) 1990 (V)–1440 (VIII); *Convolvulus arvensis* (M) 2200 (V)–1176 (IX); *Linum mucronatum* (J) 2628 (V)–1459 (VIII); *Cynodon dactylon* (M) 3350 (V)–1907 (IX).

RUDERALS, JERUSALEM. Abraham, September 1952 MS.: *Amaranthus blitoides* 450; *Erigeron crispus* 560; *Chenopodium murale* 580; *Lactuca scariola* 1500; *Inula graveolens* 1600; *Polygonum aviculare* 1900.

ROCK PLANTS, JERUSALEM. M. Zohary and Orshan, 1951: *Varthemia iphionoides* 1150 (III)–870 (VIII); *Podonosma syriaca* 1230 (VIII).

MEDITERRANEAN DUNE PLANTS, ACRE PLAIN. M. Zohary and Fahn, 1951: *Ammophila arenaria* 254 (IX); *Cakile maritima* 216 (III)–576 (IX); *Silene succulenta* 258 (III)–734 (IX); *Retama raetam* 264 (III)–636 (IX); *Tamarix gallica* 336 (III)–1020 (IX); *Artemisia monosperma* 476 (III)–492 (IX); *Oenothera drummondii* 525 (III)–1250 (IX).

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must be stated that the data it yields, when the interval between the two weighings does not exceed 2–3 min., are reliable and valuable at least as a basis for comparison, even if they do not indicate absolute values (Oppenheimer, 1947). A full discussion on this method is given by Stocker (1956), Rawitscher (1955), and Halevy (1956). Differences in the transpiration rates of different leaves of the same plant exist, of course, but these are of no more significance than the differences in the rates obtained from intact potted plants for various individuals of the same species (Pfleiderer, 1933; Orshan, MS.).

COASTAL DUNE PLANTS, NEGEV, ENVIRONS OF REVIVIM. Orshan, 1950/51 MS.: *Cyperus conglomeratus* 258 (I)–835 (IX); *Retama raetam* 270 (III)–330 (IX); *Tamarix aphylla* 432 (III)–738 (IX); *Tamarix gallica* 768 (III)–780 (IX); *Artemisia monosperma* 804 (III)–378 (IX).

INTERIOR DUNE PLANTS OF THE ARAVA VALLEY. M. Zohary and Orshan, 1956: *Haloxylon persicum* 396 (III)–696 (VI); *Retama raetam* 402 (III)–234 (IX); *Calligonum comosum* 456 (IV)–300 (IX).

MEDITERRANEAN MAQUIS AND FOREST PLANTS, NEAR HADERA (H). M. Litvak, 1953 MS.; JERUSALEM (J) Poljakoff, 1945; MOUNT CARMEL (C) Orshan, 1949/50 MS.: *Genista sphacelata* (C) 186 (VIII); *Olea europaea* (J) 82 (III)–231 (IX); *Pinus halepensis* (C) 312, 298 (VIII); *Calycotome villosa* (C) 362 (VIII); *Pistacia lentiscus* (C) 300 (V)–532, 223 (VIII); *Ceratonia siliqua* (C) 510, 411 (VIII), (J) 335 (III)–244 (IX); *Quercus calliprinos* (C) 678 (VIII); *Rhamnus palaestina* (C) 810 (V)–840 (VIII); *Crataegus azarolus* (C) 870 (VIII); *Quercus ithaburensis* (H) 850–1000 (VI); *Amygdalus communis* (J) 2200 (III)–884 (VIII).

MEDITERRANEAN BATHA AND GARIGUE PLANTS, JERUSALEM (J) Abraham, 1949/51 MS.; MOUNT CARMEL (C) Orshan, 1949/52 MS.; all figures, unless stated otherwise, are maximum rates for August: *Asparagus aphyllus* (J) 162; *Salvia triloba* (C) 336; *Cistus villosus* (J) 456; *Thymus capitatus* (J) 462 (VII); *Poterium spinosum* (J) 654; *Satureja thymbra* (C) 696; *Teucrium polium* (J) 816.

PLANTS GROWING ON THE LOESS SOIL OF THE NEGEV, HATZERIM (H), BEERSHEBA (B). Orshan, 1950 MS.: *Salsola autrani* (B) 336 (IX); *Achillea santolina* (H) 1116 (III); *Hordeum sativum* (H) 1302 (III); *Triticum durum* (H) 1308 (III); *Trigonella arabica* (H) 1632 (III).

IRANO-TURANIAN HILL PLANTS, NEGEV, ENVIRONS OF REVIVIM. Orshan, 1949/51 MS.: *Haloxylon articulatum* 180 (III)–150 (IX); *Anabasis articulata* 192 (III)–78 (IX); *Artemisia herba-alba* 306 (III)–126 (IX); the same 424 (III)–468 (X); *Noëa mucronata* 600 (V)–138 (IX).

HAMMADA PLANTS NEAR MASHABIM, IN THE NEGEV. M. Zohary and Orshan, 1954: *Zygophyllum dumosum* 210 (III)–318 (VIII); *Gymnocarpos fruticosum* 528 (III)–930 (VII); *Helianthemum kahiricum* 936 (III)–822 (VII); *Reaumuria palaestina* 618 (III)–522 (VIII); *Atractylis serratuloides* 516 (III)–684 (VII).

PLANTS GROWING IN WADIS THAT TRAVERSE THE HAMMADA, ARAVA VALLEY. M. Zohary and Orshan, 1956: *Anabasis articulata* 120 (III)–72 (IX); *Ochradenus baccatus* 204 (III)–240 (IX); *Zilla spinosa* 606 (IV)–294 (VIII); *Acacia raddiana* 1230 (VIII).

HALOPHYTES OF THE DEAD SEA REGION. Shmueli, 1948: *Tamarix tetragyna* 792 (X); *Tamarix gallica* 516 (X); *Arthrocnemum glaucum* 208 (I)–222 (VIII); *Suaeda monoica* 366 (VII); *Nitraria retusa* 212 (I)–342 (VIII); *Suaeda palaestina* 148 (VIII); *Alhagi maurorum* 491 (III)–840 (VIII); *Prosopis farcta* 820 (III)–1570 (VIII).

The above figures are recorded for comparison only. For details and yearly and daily curves the reader is referred to the original papers mentioned above. The data quoted also represent a hydroecologic cross section showing the hourly transpiration rate of the leading plants in different habitats during the dry summer season. According to these summer values we can subdivide the examined species into groups of plants with high, medium, and low rates of transpiration. To the first category belong those with summer transpiration values exceeding 800 mg./g.h., while plants in the third group have a rate of below 400 mg./g.h. The figures do not reflect the absolute water output of the whole plant, nor do they disclose the potential transpiration rate of plants under various conditions of water supply.

Summary of Observations on Transpiration. On comparing recorded readings of transpiration for plants of various habitats, the following can be summed up:

1. All hydrophytes examined have high transpiration rates. There can be no doubt about this being due to the high moisture content of the soil and the high summer temperatures prevailing in their habitat. The differences in the rates of different species should be accounted for by their inherent structural and physiologic characteristics.

2. The transpiration rates of the examined segetal plants are also high. Most of them root in the deeper layers of the alluvial soils, where moisture is plentiful during summer. However, under less favorable conditions of moisture, the water output of segetals also remains high. This is illustrated by species such as *Carthamus tenuis* and *Linum mucronatum*, growing in the shallower soils of mountain terraces. Their persistently high rate of transpiration is probably made possible by the extreme reduction of the transpiration surface, effected by a replacement of winter leaves by smaller summer leaves or by the dying off of the majority of winter leaves.

3. Rock plants, too, have a fairly high water output. It has been shown that the soft rock into which the roots of these plants penetrate may have a field capacity of as much as 22 per cent. The percentage of available moisture is presumably rather high in summer.

4. Ruderal plants are less homogeneous in their transpiration rates. Of the six plants examined, three show high and the others medium rates.

5. Coastal dunes are a favorable habitat because of the low wilting coefficient of the soil and the high water reserves of the deeper layers into which the roots of all the plants of this habitat may penetrate. Yet the plants differ markedly from one another in their transpiration rates, although they grow in more or less homogeneous soil conditions.

6. Transpiration rates of maquis and forest species are of particular interest. From the observations cited as well as from many other data at our disposal, the following conclusions can be drawn. The water output of most of the deciduous trees is high, while that of the evergreens is low to medium. Extremely low figures have been recorded for *Pinus halepensis* and *Olea europaea,* among others. The fairly wide range in the transpiration rates of these and other evergreens has already been shown by Rouschal (1938a). Recording transpiration rates in Dalmatia, he obtained the figures 1023 (mg./g.h.) for *Phillyrea media,* 717 for *Olea europaea,* and 283 for *Laurus nobilis,* where conditions were favorable. For the same species growing under drier conditions he recorded the figures 316, 208, and 96, respectively. In Palestine, too, widely varying rates were recorded for these and other trees of maquis. Although such differences are no doubt due to differences in soil moisture, none of these evergreens exhibit a high rate of transpiration. Deciduous trees that grow side by side with them also vary in their respective rates of transpiration, but the figures for deciduous trees are high, almost without exception. The differences seem to be of a genetic nature and are most probably based on structural dissimilarities in the plants. Width and arrangement of vessels—or of tracheids in coniferous trees—prove to be decisive factors. The velocity of water conduction is faster in ring-porous deciduous trees than in sclerophyllous evergreens or conifers. The marked differences in transpiration rate between specimens growing side by side can be understood only by the fact that individual plants differ from each other in their root dimensions and the accessibility of rock fissures to the deeper roots.

7. The transpiration rates of batha and garigue species are extremely uneven, but differences in the rates between species are no higher than those between individual plants of the same species in

various habitats or even in the same habitat. The extreme figures recorded for *Cistus salvifolius*, for example, were 456 and 155, respectively; in *Satureja thymbra* the extreme readings were 696 and 320; in *Salvia triloba* 336 and 155, and in *Poterium spinosum* 654 and 366, respectively. This may be explained by the fact that the soil layer which overlies the rock is generally very shallow and by the fact that fissures and soil pouches occasionally occur in the rock. Some individuals reach these deep pouches with their roots and others remain at the upper layer of the soil, which approaches the wilting coefficient very closely during summer. Thus, competition exists between individual plants for soil moisture and this is no doubt reflected in the noticeable transpiration differences between species and individuals.

8. The halophytes of the Dead Sea region can be subdivided in regard to transpiration into two ecologic groups: true halophytes and ground-water plants. In some of the habitats of true halophytes, e.g., *Suaeda palaestina, Nitraria retusa, Suaeda monoica, Arthrocnemum glaucum*, and others, there is an increase in the salt concentration of the upper soil layers during summer, and in others there is not. The low rate of transpiration and the high concentration of cell sap do not necessarily indicate difficulties in water supply but are common to succulent halophytes in general. Ground-water plants (*Prosopis, Alhagi, Tamarix*) have exceedingly deep roots and it can be presumed that they reach underground fresh water bodies, which accounts for their high transpiration rates and their comparatively low osmotic values.

9. Desert chamaephytes have a low or a medium rate of transpiration. In some the transpiration surface is reduced in summer to one eighth of the winter surface, enabling the plants to decrease their water output considerably.

Osmotic Values of Cell Sap. Osmotic pressure has been examined in many plants by the cryoscopic method (Walter, 1931). The following values are found in the leading plants of local communities:

1. Hydrophytes. Maximum values do not exceed 10 atm.; no marked seasonal differences have been noted (M. Zohary and Konis MS.).

2. In segetals the following values have been recorded: *Convolvulus arvensis* 11–20.4 atm.; *Prosopis farcta* 11.7–23.7 atm.; *Cynodon dactylon* 18.1–24.4 atm.; *Alhagi maurorum* 10.6–18.2 atm. (All data are for May and August, respectively.) The maximum value recorded thus far is 24.4 atm. (in *Cynodon dactylon*), the minimum value 7.2 atm. (in *Convolvulus hirsutus*). All data from Abraham (MS.).

3. Batha and garigue plants. Ten species have been examined. The maximum summer figure was 22.6 atm. (in *Teucrium polium*), the lowest summer figure 13 atm. (in *Satureja thymbra*). The data are supplied by Orshan (MS.) and Abraham (MS.).

4. Dune plants. Seven species were examined (M. Zohary and Fahn, 1951). The minimum winter value was 9.7 atm. (in *Silene succulenta*), and the maximum winter value was 16.8 atm. (in (*Retama raetam*). The minimum summer value was 11.7 atm. (in *Oenothera drummondii*), the maximum summer value 22.6 atm. (in *Artemisia monosperma*). In all plants examined throughout, summer values were higher than the winter ones.

5. Considerably higher osmotic values were observed by Orshan (1952 MS.) in coastal plants that are exposed to sea salt spray and that inhabit elevated shore slopes. The minimum summer value was 26.4 atm. (in *Atractylis flava*), while the maximum amounted to 62.6 atm. (in *Euphorbia paralias*).

6. Maquis and forest plants. According to Orshan (1949/50 MS.) and Poljakoff (1945), two groups can be distinguished with regard to their osmotic values:

a. High-pressure plants with summer values exceeding 30 atm., e.g., *Rhamnus alaternus* 39.2 atm., *Phillyrea media* 40.1 atm. (both in July), *Olea europaea* 42.6 atm. (November).

b. Low-pressure plants with summer values below 30 atm., e.g., *Cercis siliquastrum* 19.9 atm., *Pistacia palaestina* 21.8 atm., *Arbutus andrachne* 26.6 atm., *Laurus nobilis* 27.2 atm., with all recordings made in July; *Pistacia lentiscus* 19.6 atm., *Ceratonia siliqua* 20.2 atm., *Quercus calliprinos* 20.3 atm., *Rhamnus palaestina* 23.1 atm., *Pinus halepensis* 24.9 atm., *Crataegus azarolus* 29.6 atm., with all recordings made in August. These data indicate that there are no sharp differences between evergreen and deciduous trees with regard to their osmotic values. Yet plants with the highest osmotic values are found only among the evergreens.

7. Steppe and desert plants. Only a few of the many data are recorded here (M. Zohary and Orshan, 1954 MS.): *Zygophyllum dumosum* 25.8 atm. (March)–64.9 atm. (October); *Salsola villosa* 27.4 atm. (February)–45.9 atm. (August); *Reaumuria palaestina* 39.8 atm. (March)–203.5 atm. (October); *Anabasis articulata* 45 atm. (May)–65.9 atm. (September).

These are leading plants of the most common associations of the Negev. High summer values and considerable seasonal differences in osmotic pressure are typical here.

8. Dead Sea region halophytes (Shmueli, 1948; M. Zohary and Orshan, 1949): *Salsola rosmarinus* 27.5 atm. (March)–39.6 atm.

(October); *Salsola tetrandra* 28.6 atm. (February)–113.8 atm. (August); *Suaeda palaestina* 36.2 atm. (February)–87.2 atm. (August); *Arthrocnemum glaucum* 50.4 atm. (March)–64.5 atm. (June).

9. Desert wadi plants of the Arava Valley (M. Zohary and Orshan, 1956): *Zilla spinosa* 7.2 atm. (March)–15 atm. (September); *Acacia raddiana* 13 atm. (October); *Ochradenus baccatus* 13.0 atm. (February)–22.5 atm. (January).

INTERPRETATION. The data recorded above may be interpreted as follows.

1. The osmotic values of plants, with the exception of halophytes, may, on the whole, serve as indicators of their water balance.

2. No inferences can be made as to osmotic values without taking into account soil moisture, soil salinity, root habits, and transpiration intensity. As a rule, osmotic values of plants change with the availability of soil moisture in the same plant and in the same habitat—in various seasons and at various times of the day. There is no doubt that up to a certain limit the increase of osmotic values in plants parallels the osmotic value (suction power) in soils. Consequently, at least in xerophytes, moisture intake by the roots is to a certain extent facilitated by the rise in osmotic values of cell sap.

3. The extremely high osmotic pressures recorded among halophytes do not necessarily indicate difficulties with water supply, although they are accompanied by low transpiration rates. In this case the low rate of transpiration may be a physiologic characteristic similar to that found in non-halophytic succulents. Accumulation of salts rather than moisture deficiency causes these high values.

4. Plants growing under optimal moisture conditions, such as hydrophytes, segetals, deep-rooting trees and shrubs of alluvial soils, generally exhibit high summer transpiration rates and lowest osmotic values. Plants with a low osmotic pressure, on the other hand, do not necessarily exhibit a high rate of transpiration. The aleppo pine and the carob tree, for instance, are comparatively low-pressure plants but also have low rates of transpiration.

5. Differences in the osmotic values of species growing in the same habitat do not always reflect corresponding differences in their water supply. For instance, the osmotic pressures recorded in maquis and forest trees under more or less identical conditions of moisture were found to differ widely from one another. In this regard one can hardly compare maquis trees or Mediterranean dune plants with desert plants, which, despite effecting enormous reduc-

tions of their transpiration surface, almost double or triple their osmotic values in the dry season.

6. Batha and garigue plants resemble desert plants in their seasonal increase of the osmotic values, and in the decrease of their transpiration rate and transpiring surface. On the whole, however, their osmotic values are lower than those of desert plants.

Water Saturation Deficit. A plant's immediate response to a deficient water supply is the loss of water from its cells. Most plants observed suffer temporary water deficits, and desert plants in particular withstand very high water deficiencies for prolonged periods.

In forest and maquis trees the following maximum saturation deficits were recorded (Z. Berlinger, 1955 MS.): *Pinus halepensis* 14.7%, *Quercus calliprinos* 18%, *Phillyrea media* 43.5% (all June); *Ceratonia siliqua* 10%, *Crataegus azarolus* 23.6%, *Olea europaea* 26.9% (all September).

In desert plants the following figures were recorded: *Artemisia monosperma* 34% (April); *Atractylis serratuloides* 47.6%, *Gymnocarpos fruticosum* 52.6%, *Zygophyllum dumosum* 57.8% (all July); *Retama raetam* 20%, *Anabasis articulata* 30%, *Noëa mucronata* 33%, *Artemisia herba-alba* 65% (all August); *Reaumuria palaestina* 28.4%, *Helianthemum kahiricum* 49.5% (both September).

Poterium spinosum, the main batha species, showed a water saturation deficit of 44.8% and *Podonosma syriaca*, a leading rock plant, 27.5%; both readings were taken in October.

The problems which arise in regard to saturation deficits are of the maximum deficits that can be endured before plant activity ceases, the length of the endurance of what is called sublethal deficits, and the nature of the plant's recovery from them. Preliminary examination has shown that desert plants withstand high deficits throughout the dry season, and that the daily deficits are only partly recovered at night. It was found, for instance, that in *Zygophyllum dumosum*, the most typical desert plant, transpiration on summer days start at 6:30 A.M. with a saturation deficit of 46% in the leaves, while by 16:00 P.M. on the same day the deficit has increased to 55%. Other plants seem to behave similarly. Deficits sometimes prevail not only during the dry season but all year, as was observed in the case of *Chenolea arabica* and *Artemisia monosperma* and other plants (Evenari and Richter, 1937). The partial recovery of the deficits at night is mainly effected by a subterranean moisture supply by the roots and partly by dew deposited on the leaves. Although the quantities of dew moisture absorbed by leaves are minute, they may be of utmost importance in keeping the deficits

within safe limits. The question as to whether the resistance to high saturation deficits is peculiar to desert plants is to be answered in the affirmative, although our data show that high deficits also occur in Mediterranean plants, such as *Poterium* (44.8%) and *Phillyrea* (43.5%).

In concluding the data on the water relations of local plants, stress is laid on the following points:

1. Taking into consideration the quoted data pertaining to transpiration, one can hardly agree with the view advanced by Stocker (1933, 1935) that there is no relation between habitat and transpiration. M. Zohary (1954) shows clear differences in the summer transpiration rates of various plant communities. This difference becomes particularly striking when the chosen dominant (broader column of Fig. 68) and subdominant plants of each community are those that display the highest percentage of permanent plant coverage. Comparing various plant communities of the desert with those of the Mediterranean region, one comes to the conclusion that the late summer transpiration rate in Mediterranean plant communities is strikingly higher than in desert communities.

2. The plant's water output cannot be inferred from its transpiration rate alone, the latter however may indicate the relative water output in various plants which exhibit more or less equal transpiring surfaces.

3. The means of balancing moisture intake and output by plants vary with the habitat and the plant. These means are: (a) efficient exploitation of soil moisture by root faculties, such as dimensions, depth, and direction of growth; (b) temporary closure of stomata; (c) decrease in transpiration intensity; (d) reduction of transpiring surface; and (e) endurance of temporary water deficits.

Quantitative measurements of the intake/output ratios of plots of vegetation have yielded a positive balance both in mesic and xeric habitats, with the only difference being that in mesic habitats there is a permanent supply of available water, while plants in xeric habitats exhaust all or almost all available soil moisture before the rains fall.

4. Root dimensions are of primary importance in the maintenance of a positive water balance, provided they operate in soil layers with available moisture. The shallow root branches of many Mediterranean trees, for instance, seem to be of no hydroecologic value in summer. The summer transpiration rate of these plants is largely determined by their deep vertical root branches. The morphologic types of the root system are by themselves of minor ecologic interest, unless they are related to moisture availability in the various soil

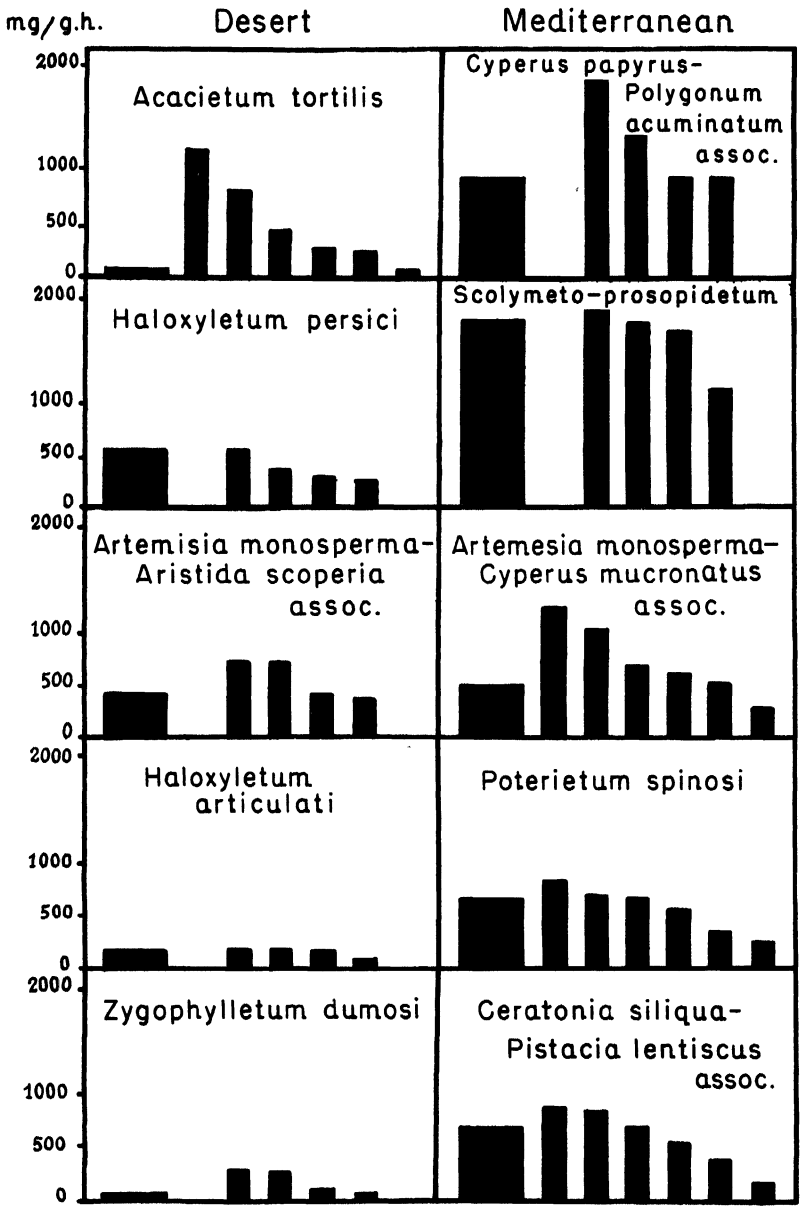

Fig. 68. Late summer transpiration rates of dominant (broad columns) and high coverage (narrow columns) species in typical Mediterranean and desert plant associations of Palestine.

layers. The most important low shrubs of the desert have shallow root systems that spread horizontally in the upper soil layer, which is the only layer into which rain water penetrates. On the other hand, desert perennials that grow in or near wadis or water runnels always have deep roots.

5. Reduction of the transpiration surface is one of the most common and most efficient means of withstanding shortage of water supply during summer. In fact, the majority of the dwarf shrubs reduce their transpiring surface considerably. The extent of the reduction differs with species and the moisture conditions of the soil. In extreme cases, e.g., *Zygophyllum dumosum*, it has been observed that 83% of the plant's transpiring organs are dropped early in summer (Orshan, 1954). Ecologists investigating factors promoting drought resistance in desert vegetation have often overlooked this fact. Significant, too, is the time at which these morphoecologic changes in the plant body occur. In less arid districts of the country morphologic changes of the plant body may occur regardless of climatic phenomena, but they correspond with seasonal changes in moisture conditions in the drier parts.

From the data presented above, it is evident that there is a considerable decrease in the summer transpiration rate of many plants growing within dry habitats. Still more striking is the absolute decrease of the water output in summer, caused by large-scale surface reduction in plants of dry habitats. These facts do not agree with the attributes ascribed to xerophytes by Maximov (1929). They come nearer to illustrating the older view on xerophytes as represented by Pfeffer (1897), Schimper (1898), and others.

No less contradictory to Maximov's view is the fact that among the permanent desert vegetation there are no plants "with a capacity of enduring wilting without injury," a feature which Maximov stresses as being most characteristic of xerophytes. What is very striking in desert plant life is that many plants of the permanent vegetation though greatly reduced in surface during the dry season are physiologically active all year; some flower or set fruit at the end of summer. In cases of very extreme drought the plants die away in masses or cease their activity and assume a state of dormancy. All this calls for a revision of our concepts of the water ecology of desert plants.

9

Man and Vegetation

Man's interference with natural vegetation is manifested in a variety of ways. Among others, there is direct extermination of plants and plant communities through excessive use. This is followed by spontaneous plant immigration from adjacent areas. Furthermore, man replaces natural habitats by artificial ones and so brings into existence new plant communities. Man also introduces along with cultivated plants and weeds a series of adventitious plants, which sometimes exterminate indigenous ones.

It is a common belief that the activities of primitive man during his hunting and plant-gathering periods did not affect vegetation to any great extent. Those periods lasted thousands of years, however, and agriculture though primitive slowly evolved within their time span. One must date back the beginnings of man's effect on vegetation in Palestine to the epoch of Natufian culture, that is, to approximately 8000 B.C., a time long before the Mesolithic period (Garrod and Bate, 1937). With the development of sedentary farming, large stretches of woodland were turned into arable land, resulting in the disappearance of large areas of arboreal plant associations. In certain places of the Mediterranean territory the rooting out of vegetation has brought about soil erosion to such an extent that hundreds of square miles in the midst of a potential woodland area have become bare rocky outcrops. In such areas villages have been abandoned because of soil loss.

Where closed plant communities of the Mediterranean territory were destroyed or their equilibrium upset, plants from adjacent steppe and desert regions spread into these communities. Furthermore, the local Mediterranean weed flora is exceedingly rich in steppe and desert species which have infiltrated into the woodlands during the millennia of agricultural history. The primitive farmer, unversed in the practice of weeding, cultivated them reluctantly

with his crop plants. These weeds have established themselves in well-defined communities.

Man is no doubt responsible for the expansion of existing lithophytic habitats, for remobilization of fixed dunes, for the formation of many ruderal plant communities in his neighborhood, and for preventing hydrophytic plant communities from overgrowing water bodies.

Man's intrusion into the steppe and desert vegetation, and his uncontrolled fuel gathering and grazing of his herds through thousands of years have left their mark on the composition of these vegetation types. Yet they have been less radically altered than the Mediterranean one. Much can be learned from the present make-up of certain plant communities about the methods of selective destruction. For instance, large stretches of ARTEMISIETUM HERBAE-ALBAE were deprived of *Artemisia* because it is easily removed and used as fuel.

There were periods in the history of Palestine when man's interference was slowed down or ceased, and a reshuffle of vegetation could take place. This happened time and again in periods of agricultural recession caused by war and exile. The forest occupied abandoned villages and cultivated ground. The remains of human habitation, such as buildings, oil and wine presses, cemeteries, and olive groves, found in the midst of dense forests, illustrate this tendency. On the other hand, in the course of thousands of years of crop husbandry, man has introduced into this country hundreds of species of cultivated plants and has replaced a great part of the primitive vegetal scenery with an artificial one.

In conclusion it must be emphasized that the scope of human infringement upon vegetation has been greatly underestimated. The following paragraphs enumerate the main aspects of such human activity affecting the flora and vegetation in Palestine.

Destruction of Vegetation by Man

The destruction of forest cover by man was a slow, selective process which depended both on his ability to overcome natural obstacles and on the tools of destruction at his disposal. Damage was done to forests in four ways: the hewing of wood for industry and fuel; grazing and browsing by goats and sheep; clearing of forest areas for tillage; and forest fires, planned or accidental. Wood was used not only for timber and the manufacture of agricultural implements and other utensils, but also for domestic and commercial fuel, i.e., in lime kilns and charcoal production. This involved extremely heavy damage to forests. Until the last decade, charcoal

was extensively used in all cities, even though other fuels were readily available. The environs of Safad, Haifa, Jerusalem, and Hebron, which were the centers of charcoal production and marketing, have been completely denuded of forest vegetation. The same is true of the hills of Samaria, where the name of a village, Umm-el-Fahm, or "Mother of the Coal," recalls charcoal production. Everywhere in Palestine devastated areas are found in the neighborhood of lime kilns.

Moreover, local trees not only provided timber for local needs but were also occasionally exported to neighboring countries. Palestine's nearness to vast stretches of timberless deserts, whose inhabitants were unversed in the care of forests, caused much of the damage resulting from mistreatment of local forests. One of the testimonies to such abuse is a wood of wild *Pistacia atlantica* in Gilead, to the east of Wadi Waran. It comprises big trees which were partly burnt at the bottoms of their trunks, showing the imprint of repeated, unsuccessful attempts at felling.

Grazing, though unable to bring about the total destruction of forests, does involve extensive deformation. Continuous browsing by goats damages young bud-bearing branches and, like pruning, results in the production of bushy growth instead of the establishment of a tree habit. Indeed, we believe that this is the only factor which has prevented the development, under optimal Mediterranean conditions, of a high forest (Hochwald), and has produced maquis instead.

However, the most devastating effect on forests is undoubtedly due to the converting of woods into arable land, a process which continues to the present day. The forest is either burned first or the trees are hewn before the roots are removed. Such clearing demands immense efforts, and every piece of hilly ground prepared for cultivation requires a considerable investment of labor and time. This is particularly so in the terra rossa region, where trunks and roots penetrate into fissures and crevices, so that their eradication constitutes an insurmountable task. Owing to this fact, the terra rossa regions of Palestine have never been made arable to the same extent as other soil types. As a result, it is mainly on terra rossa that one still finds well-developed maquis.

The conversion of rendzina in the hill region to arable land was more successful, for this soil develops from and overlies soft or even crumbling rocks. On such soils forests of *Quercus ithaburensis* and *Pinus* and also of *Quercus calliprinos* are easily eradicated. Thus in extensive areas of rendzina in the heart of the Mediterranean region

(Galilee, Samaria, Judean Mountains) that have been under cultivation for many years no remnants of their previous forest vegetation are found. Arab villages in Judea, Galilee and Samaria are largely located on rendzina. On the alluvial soils in the valleys it was even less of an effort to clear the forest and thus make the land suitable for agriculture and there also the forest has been completely annihilated. These areas today form Palestine's major granaries, as they most probably did in earlier periods. In the Sharon Plain, where the soil is less productive and where wide stretches were covered by swamps and mobile dunes, impressive stands of a *Quercus ithaburensis* forest were preserved until the beginning of this century. Most of these were destroyed during World War I.

References in the Bible and the Talmud indicate that the clearing of the forests is an ancient practice. In Joshua (16, 17) one reads: And Joshua answered them: "If thou be a great people, then get thee to the wood country and cut down for thyself . . ."

The widespread destruction of forests by man was evidently not incompatible with the adoration of trees and the great respect in which they were generally held. Trees were the symbols of godliness, of divine power. *Alon*, the Hebrew word for oak, *Ela*, the word for terebinth, and later *Ilan*, a collective name for trees in general, are all derived from *El*, the name of God. It was in the shade of trees that the judges of old gathered to dispense justice, and there services were held and the gods of many tribes were worshipped. Even to this day, Arab chiefs are buried in woods, just as in Biblical times. The so-called "sacred woods," which are secluded and protected against cutting or damage of any kind, are very common here, as in the entire Near East. Sacred trees are often recognized by the numerous pieces of cloth hung on the branches by visiting Arabs. Such holy trees are generally named in honor of the grave that they once protected and that has since vanished. As a rule, they are conspicuous by their size. Thus some holy oaks (Fig. 69) have a trunk circumference of 2–3 m. and a crown whose circumference measures up to 20 m. In deserts, where no trees are available, even bushes may become thus sanctified. Under the canopy of these holy trees the fellah leaves his belongings, his donkey and his sacks of wheat, for nobody will steal them.

Both the Bible and Talmud abound in tales referring to the life of trees, and the honor extended to trees is reflected in names of both persons and villages, such as Beth-ha-Ela—House of the terebinth; Aloney Mamreh—Oaks of Mamreh; Beth-ha-Shitta—House of acacia; Dafna—Laurel; Beth-ha-Arava—House of the willow;

Ba'al Tamar—Husband (owner) of the palm tree; Nahal Zered—River of zizyphus. In spite of this, the planting of forest trees was not popular with the ancients.

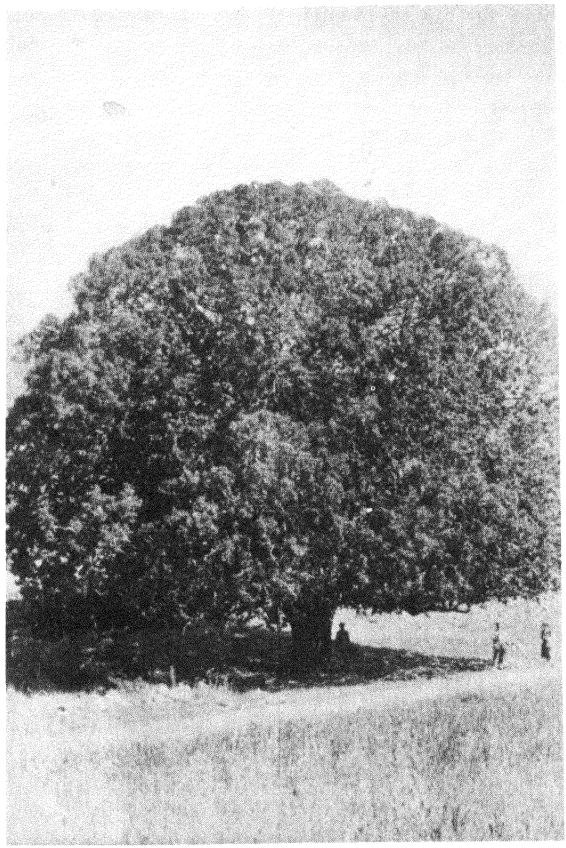

Fig. 69. *Quercus calliprinos* (sacred tree), Wadi Waran, western Gilead.

Native Plants in Everyday Use

The use of native plants by man is as old as man's history. Up to the present day there are desert tribes who ignore cultivation and obtain their vegetable nutrition from wild plants alone. Primitive man invented cultivation, one of the supreme achievements of human civilization, through long efforts at using native plants effici-

ently. The number of indigenous plants in use in Palestine amounts to several hundred and only some of them will be listed below according to their uses.

Food Plants. Many native plants used as food are collected by Bedouins and villagers not only for home consumption but also for sale at the markets. Among edible plants, the leaves and stems of the following are used as greens and salads: *Rumex roseus, Chenopodium* spp., *Isatis aleppica, Diplotaxis acris, Sisymbrium irio* and other crucifers, *Eryngium creticum, Malva rotundifolia, Salvia* spp., *Campanula rapunculus, Centaurea* spp., *Gundelia tournefortii, Lactuca cretica, Silybum marianum, Cichorium pumilum,* and *Arum* spp. The tubers or bulbs of *Erodium hirtum, Astoma seselifolium, Scorzonera papposa, Gundelia tournefortii, Hordeum bulbosum, Allium ampeloprasum,* and *Crocus hyemalis* are used as vegetable food. Spices and condiments are furnished by *Laurus nobilis, Capparis spinosa, Majorana syriaca, Calamintha incana, Satureja thymbra,* species of *Teucrium,* and others.

Edible fruits are collected, among others, from *Ochradenus baccatus, Rubus sanctus, Crataegus azarolus, Pyrus syriaca, Prunus ursina, Prosopis farcta, Ceratonia siliqua, Nitraria retusa, Salvadora persica, Zizyphus spina-christi, Z. lotus, Arbutus andrachne,* and *Lycium* spp. Numerous leguminous fruits are used as pulses, e.g., *Astragalus boeticus* and other species of this genus, *Vicia* spp., *Lathyrus* spp., *Pisum* spp., *Ervum* spp., *Lens* spp., and other leguminous plants.

Wild Bread. The seed of *Chenopodium album* growing wild here is known to have been used in years of famine and wartime for the preparation of bread. Most interesting in this regard are the species of *Mesembryanthemum,* especially *M. forskahlei,* growing in the Dead Sea region. According to Crowfoot and Baldensperger (1932), the dry, seed-bearing stalks of this plant are gathered by the desert tribesmen of Arabia and placed in water. The wetted fruit capsules open and the black seeds sink to the bottom. As the water evaporates, the seeds are collected and pounded into a hard mass, forming a type of bread. Dürkop (1903) reports that the grains of Palestine's native *Panicum turgidum* are collected in the Sahara by the natives of southern Algeria, ground, and baked into bread.

Industrial Plants. (M. Zohary and Feinbrun, 1930.)

Fiber and Wicker Plants. The wickerwork and the mat industries of the Arabs were based mainly on the supply of locally collected material of certain native swamp plants, such as *Salix* spp., *Typha angustata, Arundo donax, Phragmites communis, Scirpus* spp.,

Cyperus papyrus, Juncus spp., etc. This industry provided a means of livelihood for many families.

OIL PLANTS. There are a number of native oleiferous plants which are still grown in certain countries but are no longer under cultivation in the area comprised by Palestine. They include *Sinapis alba, S. arvensis, Brassica nigra, Calepina irregularis, Eruca sativa,* and *Ricinus communis.*

TANNIN PLANTS. Various species of *Quercus* are known to contain a high percentage of tannin in their cupules. Especially important is *Q. ithaburensis,* which is closely related to the well-known Turkish valonea oak, and whose cupules are commercially valuable and exploited. Also important are *Pinus,* the sumac (*Rhus coriaria*), *Pistacia* spp., and *Arbutus* spp.

ESSENTIAL OIL PLANTS. There are only a few plants here which are used for the extraction of essential oils, e.g., *Majorana syriaca* and *Thymus capitatus,* but there are several other local species that are being used abroad, and thus are most promising in this regard. They include species of *Salvia, Thymus, Thymbra, Micromeria, Calamintha, Lavandula,* and other members of the Labiatae which are well represented in the Mediterranean mountains. Other native plants used elsewhere for extracting essential oils are *Myrtus, Hyacinthus,* and *Narcissus.*

DYE AND SOAP PLANTS. A few wild species, known for having been used in the past as vegetable dyes, are of no present value because of the introduction of synthetic dyes. These plants are *Reseda luteola* (orange), *Tephrosia apollinea* (blue), *Echium italicum* roots (red), and *Phelypaea lutea* (yellow). The indigo plant, *Indigofera* spp., growing wild in the Dead Sea region, is perhaps an escapist of the crops once cultivated here as dye plants.

Many species of Chenopodiaceae have been widely used in the past and are still being used today, mainly in desert regions, for the production of a washing soap. In the markets of Baghdad and Damascus one finds bags of stem joints of *Haloxylon* spp., *Anabasis* spp., and various *Salsola* species. These are used as sources of potassium and have been used until recently in the manufacture of soap.

Medicinal Plants. (M. Zohary and Feinbrun, 1930.) There are a great number of native plants used chiefly in folk medicine both by the Arab population of villages and by Bedouins. While a considerable number of them are widespread in the drug markets of all the greater cities of the Near East (Cairo, Damascus, Beirut,

Jerusalem, Hebron, etc.), others are commercially rare, although they are extensively used by people who collect them. Examples of such plants are *Polygonum equisetiforme, Bongardia chrysogonum, Leontice leontopetalum, Ochradenus baccatus, Papaver rhoeas, Peganum harmala, Balanites aegyptiaca, Ruta bracteosa, Thymelaea hirsuta, Eryngium* spp., *Plumbago europaea, Calotropis procera, Alkanna strigosa, Cynoglossum pictum, Calamintha incana, Majorana syriaca, Teucrium polium* and other species of this genus, *Achillea santolina, A. fragrantissima, Inula viscosa, Artemisia herba-alba,* and *Helicophyllum crassipes.* Some herbs are used as panaceas for healing all kinds of illnesses, while others are specific. No medical proof exists as yet for the curative value of the majority of these species.

Other native medicinal plants included in older or modern pharmacopoeias are *Chenopodium ambrosioides, Laurus nobilis, Glycyrrhiza glabra, Althaea officinalis, Malva silvestris, Foeniculum vulgare, Ammi visnaga, A. majus, Nerium oleander, Salvia sclarea, S. triloba, Hyoscyamus muticus, Datura stramonium, D. metel, Valeriana dioscoridis, Citrullus colocynthis, Matricaria chamomilla, Cnicus benedictus, Anacamptis pyramidalis,* and many others.

Investigators in this field have recently started to find plants of medicinal value within the native families and genera, of which certain representatives are used in pharmaceutical practice.

Pasture Plants. (D. Zohary, 1952.) There are hundreds of palatable grass and leguminous species in the local flora which have been the source of pasture for cattle and sheep from ancient times to the present day. Overgrazing through the millennia is being remedied by methods such as the use of local species for reseeding. Among the most valuable native perennial grass species are *Dactylis glomerata, Festuca arundinacea, Hordeum bulbosum, Lolium perenne, Oryzopsis holciformis, O. coerulescens, O. miliacea, Phalaris bulbosa, Andropogon distachyus, Arrhenatherum palaestinum, Brachypodium pinnatum,* and *Bromus syriacus.* The above-named species are also well known abroad as cultivated pasture grasses.

The bulk of grazing during the rainy season is provided by annual grasses, of which the following are the most abundant and palatable: *Avena sterilis, A. barbata, A. wiestii, Bromus scoparius, B. sterilis, Cutandia memphitica, Hordeum murinum, Koeleria phleoides, Aegilops ovata, A. peregrina, A. bicornis, Brachypodium distachyum, Phalaris brachystachys, P. minor,* and *Lolium gaudini.*

Leguminous plants which grow mainly in the winter are important components of natural pastures in the months of February and March. They include, among others, *Trifolium* (about 30 species),

Medicago (about 20 species), *Lathyrus* (numerous species), *Pisum fulvum, P. elatius, Astragalus* (many species), and *Vicia* (many species).

Improvement by breeding of the palatable species found in the desert and steppe regions may provide an inexhaustible source for the development of impoverished ranges. Such plants are *Atriplex halimus, Kochia indica, Colutea istria, Crotalaria aegyptiaca, Stipa* spp., *Aristida* spp., *Panicum turgidum, Themeda forskahlei, Pennisetum dichotomum,* and many others.

Honey Plants. (Eig, 1933b; M. Zohary and Fahn, 1947; M. Zohary, 1950b.) Wild plants are the primary source of beekeeping in Palestine. There are hundreds of excellent honey plants supplying nectar, pollen, or both to the hive. Moreover, according to seasonal distribution of flowering, there is a possibility of obtaining three to four honey crops during the year. The most fruitful season, of course, is the spring, with a supply of winter annuals as well as of orange blossoms. Among the winter honey and pollen plants are *Senecio vernalis* (for early feeding), *Diplotaxis erucoides, Sinapis* spp., *Raphanus raphanistrum, Maresia pulchella* and numerous other Cruciferae, *Amygdalus communis, Trifolium* spp., *Medicago* spp., *Euphorbia cybirensis, Ridolfia segetum, Styrax officinalis, Echium judaeum,* and representatives of many other families. However, the plants of utmost importance at present are various species of *Citrus.*

In early summer bees harvest from *Daucus maximus, D. aureus, Ammi visnaga, Centaurea* spp., *Carthamus tenuis, C. glaucus, Cichorium pumilum,* etc. Midsummer bee plants are *Prosopis farcta, Eucalyptus rostrata, Thymus capitatus,* many Compositae, and others. Of the late summer plants the most important are *Inula viscosa* and a long series of other hydrophytes, especially *Rubus sanctus, Lythrum salicaria,* and *Lippia nodiflora.* Continual rotation of hives to take advantage of seasonal distribution of flowering makes Palestine one of the most favorable areas for yielding multiseasonal honey crops.

Native Plants Under Cultivation

Ornamentals. There is a series of plants growing wild in Palestine which were introduced abroad long ago as ornamentals; some are now of world-wide distribution. Examples of such annuals and perennials are *Vaccaria segetalis, Anemone coronaria, Ranunculus asiaticus, Paeonia corallina, Laurus nobilis, Glaucium flavum, Matthiola longipetala, Lupinus pilosus, Ruta bracteosa, Acer syriacum,*

Rhamnus alaternus, Cistus villosus, Myrtus communis, Nerium oleander, Vitex agnus-castus, Lippia nodiflora, Lavandula stoechas, Eremostachys laciniata, Centaurea spp., *Artemisia arborescens, Arum palaestinum, Allium neapolitanum, Lilium candidum, Sternbergia lutea, Ixiolyrion montanum, Iris atropurpurea, I. atrofusca, I. lortetii,* and *I. nazarena.*

In addition, there are a series of other native plants not at present cultivated but worthy of introduction as ornamentals for their showy flowers or other decorative properties. A few of them are some species of *Silene* and *Dianthus, Clematis flammula, Arbutus andrachne, Salvia brachycalyx, Thymbra spicata, Helichrysum sanguineum, Allium schuberti, Asparagus palaestinus, Tamus communis,* some species of *Colchicum, Crocus, Iris,* many orchids, and a few ferns.

Fodder and Forage Plants. Native species cultivated as fodder or forage plants here and abroad are *Trifolium repens, T. fragiferum, T. subterraneum, T. alexandrinum, T. resupinatum, T. clypeatum, Vicia sativa, V. narbonensis, Melilotus indicus, Erodium* spp., *Dactylis glomerata* with its many forms, *Oryzopsis miliacea, O. coerulescens, Phalaris bulbosa, Bromus tomentellus, Lolium perenne, Andropogon distachyus,* and many others. It is noteworthy that these species occur here in a variety of forms which could serve as a source for selection both on morphologic and ecologic lines.

Forest Trees. Only a few trees of the native flora are used in Palestine for afforestation. These are:

1. *Pinus halepensis.* This tree attains here a height of approximately 10 m. It is successfully grown in all Mediterranean parts of Palestine for shade, timber, and cover. Although inferior in quality when compared with the known commercial timber pines, it is extensively cultivated here and millions of these trees have recently been planted by governmental and other forestry bodies. One of the virtues of this tree is its high resistance to drought, as evidenced by its very low rate of transpiration. Several varieties of this all-Mediterranean tree exist among the local population. Only recently an ecotype has been found to grow fairly well in the western Negev under 100–120 mm. of annual rainfall. Breeding of this drought-resistant variety has only recently been started and if successful will be of great importance, since this is the only pine variety in this region that can withstand such severe conditions.

2. *Ceratonia siliqua.* This is another wild tree which has been cultivated through the ages because of the forage yielded by its pods. The wild trees were usually grafted with other cultivated

varieties yielding higher crops of pods. Recently, however, it has been extensively planted as a forest-forage tree on the more denuded hillsides unsuitable for other forest trees. Its successful growth is very promising, especially in the Mediterranean foothills. Many forms not yet sufficiently studied have been found, and investigations leading to a disclosure of drought-resistant varieties will be of supreme importance.

3. *Cupressus sempervirens.* This tree is less important in forestry. The wild-growing variety is horizontally branched. Groves of that variety have been discovered recently by Chapman (1947) in Edom and previously in Gilead by M. Zohary and Feinbrun (1955).

4. *Tamarix aphylla.* This is a common forest tree in the arid zone. It is planted in the Negev where it thrives well on sand dunes under the extreme conditions of low rainfall, but only when it is widely spaced; otherwise, it soon impoverishes the water sources and stops growing. Although it is of common occurrence in uncultivated areas, it is indigenous only in the wetter wadis of the southern Negev.

5. *Tamarix gallica.* This occurs in a variety of forms, some of which are resistant to wind and sea spray to such an extent that they can be used successfully as windbreaks. It is planted on dunes of the Negev, where it similarly requires relatively high amounts of soil moisture. Both species of *Tamarix* are easily propagated by cuttings.

6. *Quercus ithaburensis.* A few attempts have been made to plant this tree in the mountains. Since it is a comparatively fast-growing oak, it is a quite promising broad-leaved tree for afforestation.

7. *Pistacia atlantica.* This Irano-Turanian tree is very promising both as forest tree and as a stock on which *Pistacia vera,* a fruit tree, can be successfully grafted. It grows under rather poor rainfall conditions and is therefore suitable for arid zones.

Wild Ancestors of Cultivated Plants. The term "wild ancestors" is taken here to imply those taxa which are taxonomically closest to the cultivated plants in question. Future detailed investigations may be expected to elucidate the genetic relations between those ancestors and their suggested derivatives. In this respect two categories of ancestors must be distinguished:

The first category consists of plants which are specifically identical with the cultivated derivative, e.g., *Amygdalus communis, Ceratonia siliqua, Vicia sativa, V. narbonensis, Lathyrus ochrus, Trifolium alexandrinum, T. subterraneum,* and *Lupinus luteus.*

In the second group are those plants which differ morphologically from the cultivated taxa but are still closest to them taxonomically, e.g., *Beta vulgaris, Trigonella berythea, Pisum elatius, Linum angustifolium, Daucus maximus, Olea europaea* var. *oleaster, Hordeum spontaneum, Triticum dicoccoides,* and *Allium ampeloprasum.*

Man and Weeds

Geography and Origin of Weeds. No less than 450 species of weeds occur among the cultivated crops in Palestine. Some of them have been unintentionally imported together with crop seeds, and others have immigrated from neighboring steppes and deserts, while the majority are old native plants which in times prior to cultivation used to occupy open primary habitats ecologically similar to those that are now under the plough. The weed flora can be grouped into obligatory and facultative weeds.

1. OBLIGATORY WEEDS. These are confined solely to cultivated land and comprise the majority of the weed species, such as *Vaccaria segetalis, Sinapis arvensis, Raphanus raphanistrum, Diplotaxis erucoides, Bupleurum subovatum, Ridolfia segetum, Convolvulus arvensis, Galium tricorne, Cichorium pumilum, Lolium temulentum, Phalaris bulbosa, P. paradoxa,* and many others. These plants are mostly ancient weeds which have lost their primary habitats during the long history of cultivation.

Within this group there are a few species endemic to Palestine or to Palestine and Syria, e.g., *Lathyrus gloeospermus, Scandix palaestina, Astoma seselifolium, Tordylium palaestinum, Alkanna galilaea, Salvia eigii, Galium chaetopodum,* etc. These, together with the examples listed above, may be termed anecophytes, i.e., plants whose original habitat is unknown. They therefore closely resemble many of the cultivated plants which have not been found anywhere in the wild state.

2. FACULTATIVE WEEDS. This group comprises a great many species occurring both in cultivated and in primary habitats. They may be subdivided into true amphioecious and pseudoamphioecious plants. Components of the first category possess wide ecologic range and are also native to "wild" habitats. Examples of Mediterranean weeds which are components of natural plant communities in the steppes of Palestine and the Syrian Desert are *Leontice leontopetalum, Aristolochia maurorum, Vicia angustifolia* f. *amphicarpa, Malabaila sekakul, Allium schuberti,* and others. In more arid districts, for instance in sandy clay and sandy loess regions, many plants belonging to natural communities may also

occur as weeds when the land is made arable. Pseudoamphioecious weeds, on the other hand, penetrate from cultivated into the natural habitats that are temporarily under human influence, and their occurrence in the latter is entirely dependent upon man's activities.

3. Relic Weeds. These are members of primary plant communities which have been left in place by man at the time when he cleared and prepared the land. Some of them have been left intentionally for their shade or their fruit, e.g., *Ceratonia, Quercus, Zizyphus,* and *Crataegus.* Others have been preserved because man could not eradicate them by his primitive methods of cultivation, e.g., various shrubs, trees, and climbers of the Mediterranean batha, garigue, and maquis and some trees in the tropical oases of the Jordan Valley, such as *Balanites aegyptiaca, Zizyphus spina-christi,* and *Acacia* spp. Other weeds which man was unable to eradicate are the deep-rooting *Anabasis haussknechtii* in cultivated steppes, *Rhamnus palaestina* and *Crataegus azarolus* in the borderland of the Mediterranean territory, and *Acacia albida* in the coastal plain.

Many of the dominant plants of the segetal vegetation are aliens which have spread into cultivated land from habitats that differ greatly from the cultivated ones. For instance, *Prosopis farcta* and *Alhagi maurorum,* the two very deep-rooting perennials which at present dominate the entire belt of the Mediterranean cultivated alluvial soils, are at home on the banks of the Tigris, Euphrates, and Jordan rivers and on the salines adjacent to them. Similarly, *Desmostachya bipinnata,* which until recently has occupied large stretches of arable land in the sandy clay belt of the coastal plain, has its home on the salines of the Arava Valley and similar habitats in the North African Sahara and Iran. *Ononis leiosperma,* an aggressive perennial weed which is the leading plant on cultivated mountain terraces, has been found by the author as a component of natural communities in the high altitudes of Jebel Druze in southeastern Syria. It is probable that these four species are each represented by a particular weed ecotype here. Such puzzling distribution patterns are rather rare. Many weeds have a wide range of distribution, a feature which can be explained by the fact that they are almost excluded from competition and are unintentionally cultivated along with the crop plants, which largely counteracts their climatic limits of distribution.

A phytogeographic analysis of the Palestine weed flora reveals the following groups: the Mediterranean group, 177 species; the Irano-Turanian, 55 species; the Saharo-Sindian, 22; the Mediterrano–Irano-Turanian group, 132; the Mediterrano–Saharo-Sindian group,

3; the Irano-Turano–Saharo-Sindian group, 2; and the pluriregional groups, 62 species.

The manifoldness of this flora in Palestine can be accounted for by the primitive methods of cultivation and weeding practiced up to now. With the introduction of modern and intensive farming methods and systematic weed control, the distribution of a high number of weeds is being considerably reduced.

Weed Communities. (Zohary, 1950c.) The entire weed flora of Palestine, together with the ruderal plants, has been included according to Braun-Blanquet *et al.* (1936) within a single class: the RUDERETO–SECALINETEA. Although the class has recently been split by him and by other European botanists into several further classes, the author does not see any justification at present for such a subdivision of the local weed vegetation. There are, however, major floristic and ecologic differences between the weeds of irrigated and those of non-irrigated crops. Only the latter are dealt with here.

Five well-defined major communities of segetal plants can be distinguished here, each confined to a particular habitat and not altering with the cultivated crop. All occur in non-irrigated crops and each association exists in a number of variants, depending on soil type.

1. THE SCOLYMETO–PROSOPIDETUM (Fig. 70). This association is confined to the heavy soils of the plains and valleys of the Mediterranean territory. It occurs in two seasonal aspects. The winter aspect is richest in species, notably annuals, many of which are the most noxious weeds. The most characteristic winter species are *Scolymus maculatus, Convolvulus arvensis, C. hirsutus, Galium tricorne, Cephalaria syriaca, Gladiolus segetum, Coronilla scorpioides, Phalaris paradoxa, Centaurea verutum, Cichorium pumilum, Vaccaria segetalis, Ridolfia segetum, Bupleurum subovatum, Daucus aureus, Capnophyllum peregrinum, Securigera securidaca, Rapistrum rugosum, Sinapis arvensis, Brassica nigra, Phalaris paradoxa,* and *Lolium temulentum.* The summer aspect is considerably poorer and is dominated by *Prosopis farcta, Chrozophora tinctoria, Molucella laevis, Malvella sherardiana, Heliotropium europaeum, H. villosum, Linaria elatine,* and *Euphorbia lanata.*

The SCOLYMETO–PROSOPIDETUM is the most common and characteristic association in the entire belt of the alluvial soils which is today the center of intensive agriculture. Corresponding to variation in soil composition and soil moisture, some small floristic variants have been distinguished within it. In one of the variants *Prosopis* is

Fig. 70. *Scolymeto–Prosopidetum*, near Rosh-Pinna, upper Galilee.

replaced by *Alhagi maurorum;* in another, occurring on soils occasionally flooded in winter, by *Phragmites communis.*

2. THE ASSOCIATION OF ONONIS LEIOSPERMA AND CARTHAMUS TENUIS. This is another widespread community which characterizes the cultivated terraces of Mediterranean hills and mountainsides. It grows on either terra rossa or on rendzina, both of which are considerably drier than alluvial soils. The number of species in this association is rather small, the most characteristic of them being *Bongardia chrysogonum, Campanula strigosa, Specularia pentagona, Gladiolus atroviolaceus, Leontice leontopetalum, Aristolochia maurorum, Astoma seselifolium, Phalaris brachystachys, P. bulbosa, Calepina irregularis,* and *Asperula arvensis.* But the most common species are those which also occur in the *Scolymus–Prosopis* association, namely, *Sinapis arvensis, Cephalaria syriaca, Lolium temulentum, Convolvulus arvensis, C. hirsutus, Ridolfia segetum,* etc. The summer aspect is dominated by the flowering spiny summer form of *Ononis leiosperma,* a plant occurring in winter in a vegetative mesophilous form, by *Carthamus tenuis, Eryngium creticum, Hypericum crispum, Heliotropium* spp., *Chrozophora tinctoria,* and by others.

3. THE ACHILLEETUM SANTOLINAE. This weed association is characteristic of the loess soil in the northern Negev. Agriculture here is unstable and limited to winter crops, mainly barley and more rarely wheat, in a very primitive crop rotation. This weed association differs from the *Ononis leiosperma–Carthamus tenuis* in harboring a number of particular steppe and desert plants in addition to many Mediterranean ones. It has no summer aspect. According to certain soil properties, notably to varying moisture conditions, a few floristic variants have been distinguished in it. Some of the species characterizing this association are *Achillea santolina, Glaucium corniculatum, Hyoscyamus reticulatus, Leopoldia longipes, Malva aegyptia, Salvia lanigera, Onopordon alexandrinum, Launaea tenuiloba, Pisum humile, Vicia monantha, Trigonella arabica, Matthiola livida,* and *Erucaria boveana.*

4. THE LEOPOLDIA EBURNEA–LOLIUM GAUDINI. This weed association marks the sandy loess soils of the western Negev, which (as already mentioned) are the most fertile of the Negev, although they do not obtain more than 100–200 mm. rain. Wheat and barley are sown in winter, and muskmelons, watermelons, and durra in summer. The most common or characteristic weeds are *Lolium gaudini, Leopoldia eburnea, Linaria ascalonica, Aegilops bicornis, Ononis serrata, Artemisia monosperma, Astragalus annularis, Hippocrepis*

bicontorta, Coronilla repanda, Colchicum ritchii, Dipcadi erythreum, and *Trisetum glumaceum.* All of these are more or less restricted within the association; other more widespread plants are *Cutandia memphitica, Lotus villosus, Cynodon dactylon,* and *Trigonella arabica.*

Many of the weeds of this association also occur in the primary vegetation of this area dominated by *Artemisia monosperma.* The segetal community of the sandy loess fields is thus floristically very close to that of the primary association of *Artemisia monosperma–Lolium gaudini,* growing in the same locality on unploughed land. The differences lie mainly in the quantitative relations of the individual species. A similar confluence of natural and segetal vegetation occurs in the loess soil and in the coastal sandy clays, as will be seen below. It may be generally concluded that the resemblance between segetal and non-segetal communities increases with the extremeness of the habitat.

5. THE DESMOSTACHYA (ERAGROSTIS) BIPINNATA–CENTAUREA PROCURRENS. This association is confined to the cultivated land in the Mediterranean coastal sandy clay belt. Floristically it only differs from the non-segetal association of the same belt (mentioned under the same name in Chapter 7) in the considerably smaller number of species and in the difference of coverage by the individual species. Well-represented species are *Ormenis mixta, Crepis aculeata, Centaurea procurrens, Brassica tournefortii, Ornithopus compressus, Reseda orientalis, Tulipa sharonensis, Lupinus angustifolius,* and *Silene gallica.*

The above five segetal communities comprise the bulk of Palestine's weeds in non-irrigated fields, orchards, etc. Each association displays a number of variants according to minor differences in habitat and also according to the specific agrotechnical methods. On the other hand, no significant differences in the floristic composition of the weed community growing with different crops have been found.

Irrigated crops have their particular weed vegetation, which is more hydrophytic in character than that of non-irrigated crops. Their phytosociologic make-up has not been adequately studied, so that only a list of the most characteristic species can be mentioned here. These are *Portulaca oleracea, Amaranthus graecizans, A. retroflexus, Cyperus rotundus, Echinochloa colonum, Digitaria sanguinalis, Corchorus trilocularis, Eragrostis megastachya, E. minor, Erigeron crispus, E. canadensis, Brachiaria eruciformis,* and *Setaria verticillata.* Some of these plants may also occur in ruderal

habitats. Geographically, they are mostly borealo-tropical heat- and moisture-requiring plants.

Weeds of Interest. The fact that certain weeds avail themselves, by way of selection, of some characters peculiar to cultivated plants, was first stressed by Thellung (1930). The weed *Bromus secalinus*, to mention an example, retains its spikelike panicle intact at maturity, and, unlike its congeneric species, this weed does not release its grains singly. This characteristic causes the weed to be harvested and thrashed together with the cultivated crop. Synchronous fruit-setting and equality in height with that of the crop plant are other features adopted by certain weeds, resulting in their seeds being resown with the crop. Other weeds simulate crop plants in the size and shape of their seeds to such an extent that they are able year after year to pass through the same sieve meshes with the grains of the crop. A number of local weeds which exhibit such features are the following.

Lolium temulentum is a common weed of wheat crops. It is a stout, poorly branched grass of the same height as wheat and matures simultaneously with it. Its spikes do not separate at maturity into spikelets or grains but remain intact and are harvested with the crop. Its grains are similar in size and shape to certain local wheat varieties and therefore are readily sown year after year with the crop grains or are ground with them. Flour containing a high percentage of *Lolium* grains is known to be bitter and even poisonous.

Cephalaria syriaca is very similar to *Lolium* in its height, synaptospermy, time of seed maturing, and the resemblance of its seeds to the grains of certain varieties of wheat. As a result, *Cephalaria* seed becomes mixed with wheat grains in the field and also in the mill, where it spoils the flour by its bitter taste.

There are several other synaptospermous weeds, such as *Bupleurum subovatum, Securigera securidaca, Capnophyllum peregrinum*, and others, which are harvested together with the crops.

Also noteworthy is *Galium tricorne*, a weed known since the Early Bronze period (Feinbrun, 1938; Negbi, 1955), which grows among crops of lentil and is also found among vetches. Its mericarps simulate the grains of lentils and vetches in their size and shape. According to Zaitschek (1957), *Galium* and *Cephalaria* seeds have been also found among vetch grains in the Israel Period (twelfth to eleventh centuries B.C.).

Among the "bersim" clover (*Trifolium alexandrinum*), *Sinapis arvensis* and *Cuscuta* spp. are the most frequent weeds, again because of the similarity of their seeds to those of the crop. *Phalaris*

canariensis has hitherto been found as a weed only among crops of flax. Again, the seeds of this *Phalaris* bear a close resemblance to linseed.

Another interesting plant is *Phalaris paradoxa,* one of the most noxious weeds on heavy soil. Its spikelike panicle consists of two kinds of dispersal units. Those on the upper part of the ear are furnished with winglike sterile spikelets which separate easily from the rhachis and are readily dispersed by wind, while those on the lower part are surrounded by wedgelike sterile spikelets and are kept on the rhachis until harvest time.

The annual *Cichorium pumilum* is also worth mentioning because it regenerates readily after being mowed together with alfalfa and clover in which it is a common weed.

Cephalaria syriaca, already mentioned, is also interesting from another aspect. It is a noxious weed throughout the Near East and a living evidence of how cultivated plants arose from weeds. Zhukovsky (1950) found this plant in Asia Minor under cultivation as an oil plant, and doubtless as one grown reluctantly, because of its suppressing influence on the wheat crop. In Palestine it is a particularly common weed in the Philistian Plain. Here, near Bror Hail, Arab peasants have harvested it as a forage plant. When asked whether the plant had been sown for that purpose, the answer was that it had been sown "by the devil." In fact, this weed was so abundant here that it crowded out the sown wheat plants.

Ruderal Plant Communities

The particular flora that occupies waste places, roadsides, dung heaps, etc., has no doubt existed here before the advent of man but has been largely extended and ecologically specialized by his activities. In fact, one also finds many ruderal plants on more or less saline soils, in wadis where plant debris accumulates, and on river banks. The number of ruderal plants is exceedingly great and their grouping into communities is very difficult because of their ecologic amplitude and because some of them also occur in segetal habitats. Only a few, more or less well-defined communities will be mentioned.

1. **Chenopodietum muralis.** This is one of the most common communities on dung and dust heaps and in devastated gardens and yards. The most characteristic species of this community are *Chenopodium murale, C. opulifolium, Urospermum picroides, Amaranthus blitoides, Erigeron crispus, Lavatera cretica,* and *Erodium moschatum.*

2. **Malveto-Hirschfeldietum.** This association is characteristic of roadsides all over the Mediterranean part of Palestine. It occupies the narrow strip between the road edge and the parallel ditches behind. The winter aspect is dominated by *Malva* and *Erodium*, and the early summer aspect by *Hirschfeldia* and *Carduus*. Some of the most characteristic species of this community are *Malva nicaeensis, Erodium moschatum, Lolium rigidum, Avena barbata, Poa exilis, Geranium molle, Hordeum murinum, Hirschfeldia incana, Carduus argentatus, Silybum marianum,* and *Centaurea iberica.*

Atriplicetum roseae. This association is found on loose heaps of debris and dust near human dwellings. A list of plants noted on a refuse heap in Jerusalem included the following: *Atriplex rosea, Amaranthus blitoides, Malva nicaeensis, Ecballium elaterium, Polygonum aviculare, Chenopodium opulifolium, C. vulvaria, Sonchus oleraceus,* and *Lactuca scariola.*

The edaphic reasons for a phytosociologic differentiation of the ruderal vegetation are not yet entirely clear. Even in Europe, where that type of vegetation has been investigated thoroughly from the viewpoint of phytosociology, no sound ecologic basis for the many plant communities seems to have been established (Tüxen, 1950; Braun-Blanquet *et al.*, 1952), and there is a divergence of opinion between authorities not only as to the delimitation of the lower units but also as to grouping of these units into higher categories. From literature on the subject it is obvious that many of the Central European ruderals are typical segetals in Palestine and are of constant occurrence among dry-farmed crops. Some other northern ruderals are found here as weeds among irrigated crops. It is also clear that camp followers, dust-heap plants, and roadside plants are not necessarily nitrate demanding, as was hitherto commonly assumed. It seems that a great many of them demand certain physical soil properties rather than chemical ones. The ruderal vegetation deserves an intensive ecologic investigation before subdivisions into plant communities on an ecologic basis can be made.

Neophytes

It is to be assumed that many "native" species have arrived in Palestine from near and distant parts in the more recent centuries. Unfortunately, no records of these "older" newcomers are available. Possibly many of them may have joined the native segetal and ruderal vegetation. *Oenothera drummondii* is not the only instance of a plant that has been unintentionally brought into Palestine and has since occupied large stretches in primary habitats of the coastal

sand dunes of the country, where it occurs in four different plant communities. There exist no exact data as to its first occurrence here, but the plant certainly could not have been introduced earlier than at the close of the last century or it would have been recorded by Boissier, Post, and others. At nearly the same time the South African *Oxalis cernua* was presumably imported into the coastal plain from North Africa together with crop seeds. It is a shade-demanding weed and is now widespread in orchards and under hedges. As a heterotristylous species of which only one race has been introduced, it fails to set fruit here and it propagates exclusively by bulbils. At its advent in Palestine, it was restricted to the coastal plain, and its migration to the mountain region, where it gains new positions from year to year, has proceeded during the last two decades.

A more recent newcomer is *Erigeron canadensis*, which was first observed in 1939 in the Huleh Plain. During the ten subsequent years it spread over the whole coastal plain and into the mountain ranges and is now widespread throughout the non-arid parts of Palestine, growing together with *E. crispus* and intercrossing with it. *Paspalum distichum* was also first found in 1939 in the Huleh swamps and is now also widespread in the swamps of the Sharon Plain. *Galinsoga parviflora* was first recorded in 1950 in the nursery of Mikveh Israel but is now rather common in waste places elsewhere. Other well-established and widespread newcomers are *Euphorbia pilulifera, E. nutans, E. prunifolia, Solanum dulcamara, S. elaeagnifolium, S. hystrix, Bidens bipinnatus, Xanthium italicum,* and *Cenchrus echinatus.*

Other interesting occurrences in the distribution of certain local plants during the last decade may be recorded here: *Kochia indica,* described from Jaffa by Bornmueller and Dinsmore in 1921 as *Bassia joppensis,* could not be found again for 27 years. In 1948 it appeared in large numbers in the northern Negev, where it was presumably reintroduced by Egyptian troops during Israel's War of Independence. It is now one of the most common ruderals in the northern Negev and is taken into cultivation as a desert forage plant. *Salsola kali* was never found in the Negev until 1948, but since then it has become rather common in the environs of Revivim and elsewhere. Until recently *Johrenia juncea* has been an exceedingly rare plant but lately it has become widespread in the mountain region in ruderal habitats.

Silybum marianum var. *albiflorum* was first found in the coastal plain and described as a rather rare variety. It has recently become very widespread both in the coastal plain and in the Judean Moun-

tains. In Jerusalem, for instance, it has almost entirely replaced the typical, pink form of this species. *Aellenia* (*Salsola*) *autrani*, which used to be common in the Jordan Valley but was very rare in the Negev, has recently become one of the most noxious weeds in the loess areas of the Negev and an obstacle to cultivation. Since 1957 it has begun to disappear, probably as a result of fungal attack.

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