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# Integrating multiple components of long-term tree population dynamics: pine expansion on Mt Pithulim

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Foundation Paper - looking into the long-term population dynamics / recruitment at Mt. Pithulim. Uses many tools to understand the population dynamics.

Keywords: tree population dynamics, spatial spread, *Pinus halepensis*, seed dispersal, seedling recruitment, spatial heterogeneity, mechanistic models, GIS, air photos, tree rings, gene flow, topsoil characteristics, microclimatic factors

ABSTRACT: Analyses of tree rings and historical air photos reveal the existence of five Aleppo pine trees on Mount Pithulim (Judean Hills, Israel) since early in the 20th century. This small population – well isolated from any neighboring population and not experiencing any planting, cutting or fire – has expanded to the thousands of trees inhabiting the site today. This provides a unique opportunity to investigate long-term tree population dynamics in a heterogeneous landscape in exceptionally fine detail. The Mt Pithulim Project integrates a diverse set of field and laboratory work, remote sensing, geographical information systems (GIS), dendrochronological methods, micrometeorological measurements, mathematical modeling and genetic analyses using several molecular techniques. As such, it represents the first interdisciplinary attempt to encompass all the major determinants of long-term tree population spread, from seed production through dispersal and establishment to adult growth and reproduction. The history of population spread has been reconstructed at the level of individual trees, and the major influencing factors, including edaphic, topographic, microclimatic and biological ones, have been mapped in 5x5 m resolution. Genetic analyses reveal gene flow patterns and parent-offspring relationships. Tree ring analyses reveal the key role of local factors such as tree density in determining growth. Field studies of seed dispersal and early establishment processes, integrated with GIS and atmospheric models, constitute the first mechanistic model of recruitment processes for any tree population.

## 1 INTRODUCTION

Spatial dynamics in plant populations involve a series of successive processes, from flowering and pollination, through seed dispersal and seedling establishment, to the survival and growth of reproductive adults. These processes often take place in heterogeneous environments, in which spatial heterogeneity, by itself and through its interactions with other processes, largely affects plant dynamics. Abundant field evidence emphasizes the critical importance of recruitment processes and spatial heterogeneity to plant dynamics; yet, experimental or observational studies elucidating their relative role are scarce, especially for trees and other perennial plants with late maturation. Forest dynamics models regularly emphasize tree growth and assume spatial homogeneity, while neglecting recruitment and spatial heterogeneity. Better understanding and more realistic description of forest dynamics require not only incorporation of recruitment and spatial heterogeneity, but also rigorous tests against well-documented cases of tree spatial dynamics in heterogeneous landscapes.

This paper presents a new project aimed at investigating the relative role of recruitment processes and spatial heterogeneity in determining spatial spread, demographic and genetic structure, in an expanding tree population. Towards this end, we study the multiple components of tree population spread in very fine detail, and employ a diverse set of ecological field, laboratory and modeling works, remote sensing, geographical information systems (GIS) and genetic analyses. This integrated interdisciplinary project is expected to provide a powerful new tool to predict tree spread, hence contribute to the management of natural and planted forests, the design of sustainable afforestation and reforestation, and the prediction of range changes due to global climatic changes.

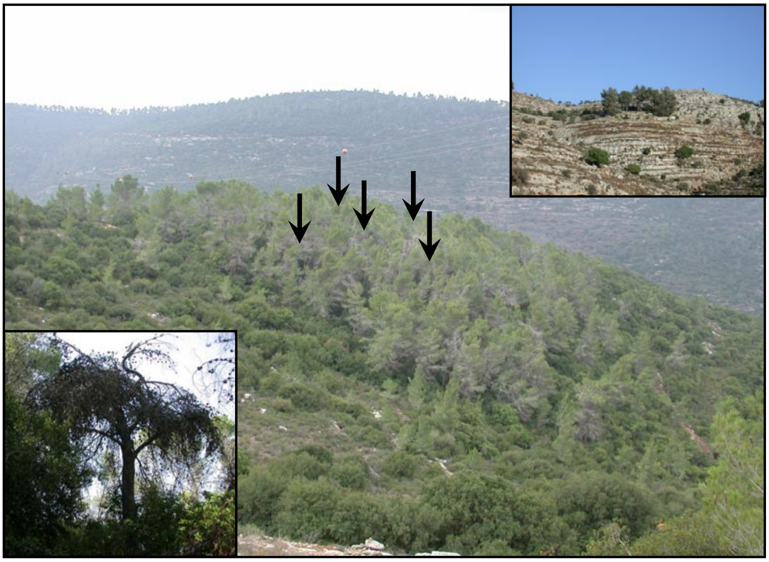

Figure 1. Aleppo pine stand on Mt Pithulim, surrounded by *Quercus-Arbutus* maquis and *Sarcopoterium-Cistus* batha. In the year 2003, this stand occupied approximately 900 adult trees and 700 more trees scattered within a 300 m radius. The trees are hypothesized to be descendants of five trees currently located at the stand center (arrows; one shown in the left insert); these five trees had established between 1880 and 1920, and may have formed an isolated cluster protected from grazing by the local farmers, as presently can be found elsewhere in the Judean Hill (e.g., near Al Walaja, about 10 km east of the study site; right insert).

## 2 THE CASE STUDY: ALEPPO PINE POPULATION ON MT PITHULIM

The selected case study provides a unique opportunity to investigate the entire set of recruitment processes that determine tree population spread in a highly heterogeneous environment over a period of 100 years. The species – Aleppo pine (*Pinus halepensis* Miller) – is the most common pine of the Mediterranean Basin (Barbéro et al. 1998) which is also common in plantations both within and outside its natural range. Because Aleppo pine is a highly invasive species (Richardson 2000), understanding the mechanisms of recruitment processes that determine its spatial dynamics is of great practical significance. The site – on Mt Pithulim at the Judean Hills of Israel (31°45' N, 35°04' E, 628 m altitude; Fig. 1) – is a typical East-Mediterranean ecosystem positioned in a complex terrain of compound lithology (see below). Mean annual rainfall is 600 mm, and mean monthly temperature ranges from 25 °C (August) to 12 °C (January). The site is occupied by a native Aleppo pine population that was isolated for a long time from any neighboring population, with no evidence for any planting, cutting or fire. This population has expanded from 5 trees at the beginning of the 20th century, to the thousands of trees that inhabit the site today. The history of this spatial spread, and of major influencing factors, is being reconstructed in exceptionally fine detail (section 4), providing a uniquely detailed long-term perspective into the dynamics of any tree population.

A 60 ha (750 x 800 m) plot was selected within the Mt Pithulim site for this project (Fig. 2), based on the following criteria: (1) should contain the core of the old dense stand (Fig. 1) and at least a 150-m buffer around it; (2) should avoid very steep terrain (>35°) in which fieldwork is extremely difficult; and (3) should represent all the major topographical and edaphic units of the site.

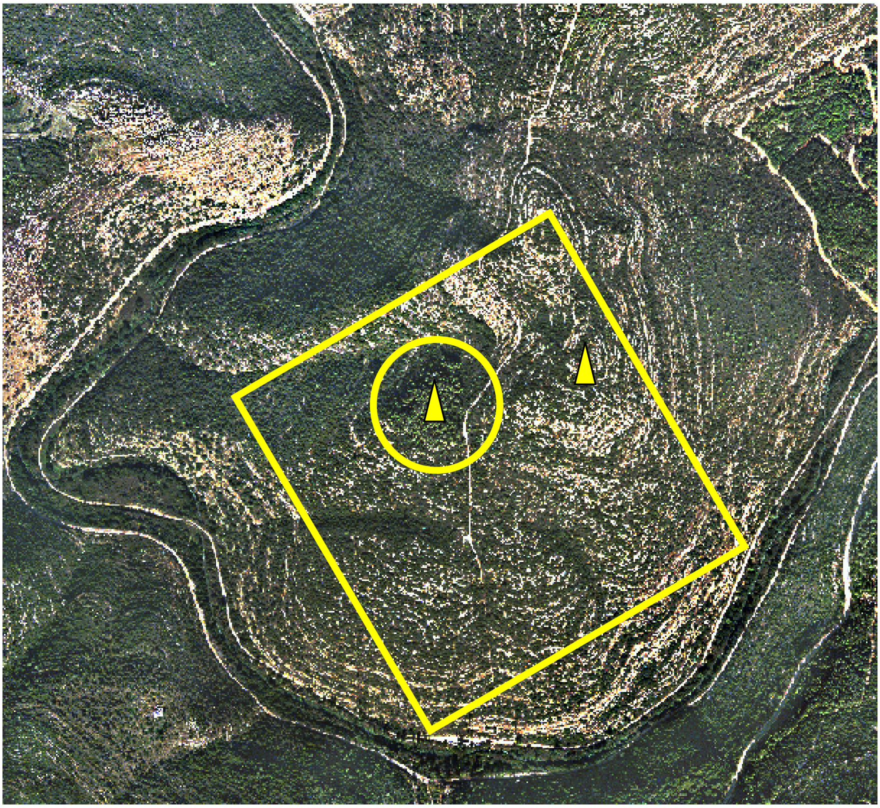

Figure 2. Orthophoto of the study site on Mt. Pithulim at the Judean Hills in Israel, prepared from an air photo taken in 1996. The rectangle indicates the 60 ha (750 x 800 m) plot. The circle indicates the location of the dense Aleppo pine stand (Fig. 1). The small filled triangles indicate the locations of two micrometeorological stations established in the site in 1997 (10 m height; right) and 2003 (24 m; left).

## 3 MAPPING AND MEASURING LOCAL FACTORS

### 3.1 *Topographic and edaphic factors*

We used a recent (2003) air photo (section 4.1) to produce a Digital Elevation Model (DEM) for the study site. Seven ground control points were identified in the photo and measured in the field using an Ashtech 5-cm resolution RTK-GPS receiver. The DEM was produced using the *Orthobase Pro* tool of the ERDAS IMAGINE image processing software. Root Mean Square Error (RMSE) of the ground control points was < 0.5 m. [A. Tsairi & T. Svoray, BGU]

Slope and aspect layers were calculated from the DEM using the ERDAS *Topographic Analysis* tool. Flow accumulation matrix was calculated based on the "eight flow direction matrix" method using the ARC/INFO *Grid* tool. Aspect data was calculated according to the distance from the north in order to express the local effect of solar radiation flux. Thus, the azimuth circle was divided to three groups: north ($300^0$-$60^0$); south ($120^0$-$240^0$); and east/west combined ($240^0$-$300^0$ and $60^0$-$120^0$). [T. Svoray].

A detailed geological map of the site (Fig. 3) has been produced based on extensive field campaign including stratigraphic mapping. Transect data were coupled with topographic maps (produced from the DEM) to create more detailed geologic maps [R. Shafran, BGU]. This stage allowed us to reveal geologic layers that were not reported in the 1:50,000 geological map of the Israeli Geological Survey. Soil samples have been taken from the top 5 cm soil layer at 30 different locations within the 60 ha plot in summer 2003 [R. Shafran]. The following topsoil characteristics have been measured in a laboratory (Gilat Experiment Station, Israel): Primary nutrients (N-nitrate, N-ammonium, P and K), micronutrients (Fe), soil pH, conductivity, soil texture (percentage of sand, silt and clay), soil moisture content, water saturation percentage and several physical soil surface features (e.g., bedrock cover, stoniness, and percentage of soil cracks). Semi-variograms of these preliminary data reveal significant spatial structure only for soil texture, soil moisture (closely associated with slope orientation) and bedrock cover [A. Mussery, HUJ]. Further soil sampling from 70 additional sites is planned for winter 2003/2004. [A. Mussery].

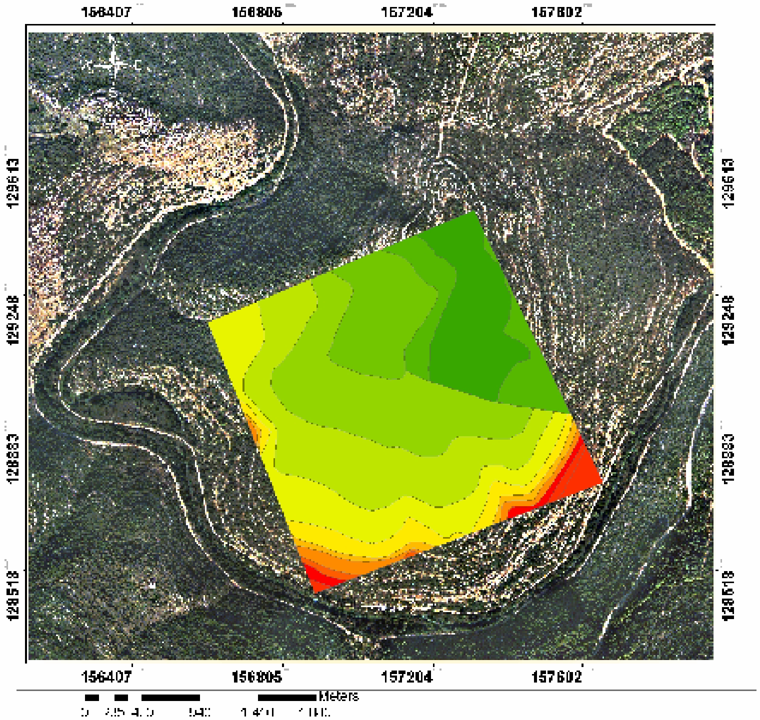

Figure 3. Geological map of the 60 ha plot on Mt Pithulim, produced based on intensive field survey and detailed DEM map. The dark green layer shows the Bet-Meir formation of dolomite with eroded clay; the green layer with the white diamonds shows the Kissalon formation of limestone, dolomite and calcite clusters; the red layers show the Givat Yaarim formation of dolomite stratified with flint and quartz clusters; all other layers belong to the Soreq formation and differ in combinations of dolomite, limestone and marl.

### 3.2 *Micrometeorological measurements*

Micrometeorological measurements were continuously recorded along a 10-m high tower on the top of the southern peak in the site (Fig. 2) during 15 months between April 1997 and June 1998 (Nathan et al. 1999, 2001). Measurements include horizontal windspeed by cup anemometers at 2 and 10 m above the ground, all three dimensions of windspeed by a UVW anemometer at 6 m above the ground, and air temperature and relative humidity at 2 m above the ground. During the year 2004 we plan to resume micrometeorological measurements along this tower, and along a new 24-m high tower established within the dense stand in summer 2003, using high-frequency and highly accurate three-dimensional ultrasonic anemometers. We shall also measure precipitation on a monthly basis, using 10 rainfall gauges placed throughout the 60 ha plot. [C. Bannai, HUJ].

### 3.3 *Pines*

Intensive fieldwork has been devoted to map the exact location, in 2.5 m resolution, of all individual Aleppo pines within the 60 ha plot having a diameter at breast (1.37m) height (DBH) equal or greater than 5 cm. A large mapping effort, assisted by sub-meter differential GPS measurements, three-dimensional laser rangefinder (measuring source-target range, bearing and inclination), and a recent (2003) high resolution orthophoto of the site, has yielded a map of ~1600 trees. This demanding field task is expected to be completed in the beginning of 2004. The expected end product of this effort constitutes a multilayer map with the following characteristics for each individual tree: location (latitude, longitude, altitude), estimated year of germination, estimated year of establishment (year first recognized in an air photo), year of death, DBH, basal area, crown projection area and height. The last 4 characteristics are dynamic parameters, whose value is likely to change with time hence depend on the year of measurement; DBH and height measurements are being determined for all trees within the 60 ha plot during winter 2003/2004. [O. Steinitz, HUJ].

## 4 THE PAST: RECOSTRUCTING THE HISTORY OF PINE EXPANSION

### 4.1 *Historical air photos*

Thirty-two historical panchromatic air photos were purchased from Israel Mapping Center, ranging from the year 1944 to 2000. An additional color air photo of the site from the year 1996 has been prepared in our previous work on this site. More recent color and panchromatic air photos of the site were taken in April 2003. From the 32 historical panchromatic photos, we selected 5 stereoscopic pairs of photos from the years 1949, 1956, 1963, 1974 and 1986, covering, together with the 1996 and 2003 color photos, one stereoscopic pair per decade since the 1940s. The panchromatic and color photos were scanned by a photogrametric scanner at 1600 and 2400 dpi resolution, respectively. The scanned photos were rectified using the ERDAS *Orthobase Pro* tool (section 3.1), using 7 ground control points with a total RMSE of less than 0.6 m for any decade [A. Tsairi, T. Svoray]. The spatial resolution of the resulting orthophotos (Fig. 4) is between 0.2 and 0.3 m. For each decade, we shall determine the number and location of adult trees by combining data on the present (2003) location of each tree (section 3.4) and stereoscopic inspection of trees by means of the ERDAS *Stereo Analyst* tool, using the tree ring data (section 4.2) for validation. [O. Steinitz].

### 4.2 *Dendrochronology*

The existence of clear annual rings in Aleppo pine (Lev-Yadun 2000) provides the means to estimate the year of germination and the rate of tree growth during the study period. Because the field and lab work required for obtaining and analyzing core samples from all 1600 trees is enormous, tree-ring analyses cannot serve as the basic tool for reconstructing pine expansion history; rather, age estimated from tree-ring data for a sample of trees will be used to test the pine expansion history reconstructed from air photos (section 4.1). For this purpose, we selected a sample of 180 trees, including the 5 oldest trees within the stand, 115 trees that have been suspected to be the oldest among all other trees, and 60 trees that have been selected in random to represent the major topographic-edaphic units of the site [C. Bannai & D. Troupin, HUJ]. Cores are being extracted by a mechanical increment borer and cross-dating is assisted by the COFECHA software (Holmes 1983). Age determination is especially difficult for the five old trees of which one is barely alive, three are standing dead, and one has fallen during a snowstorm. Complete cross section taken from the trunk of this fallen tree revealed 1917 as the estimated year of germination. According to earlier dendrochronological works carried out in the site during the 1970s, one of the remaining old trees has been estimated to germinate during the 1880s (Y. Waisel, TAU, *Personal Communication*). A preliminary analysis yielded that at least 24 trees (and probably many more), have been germinated between 1940 and 1960. [C. Bannai & D. Troupin].

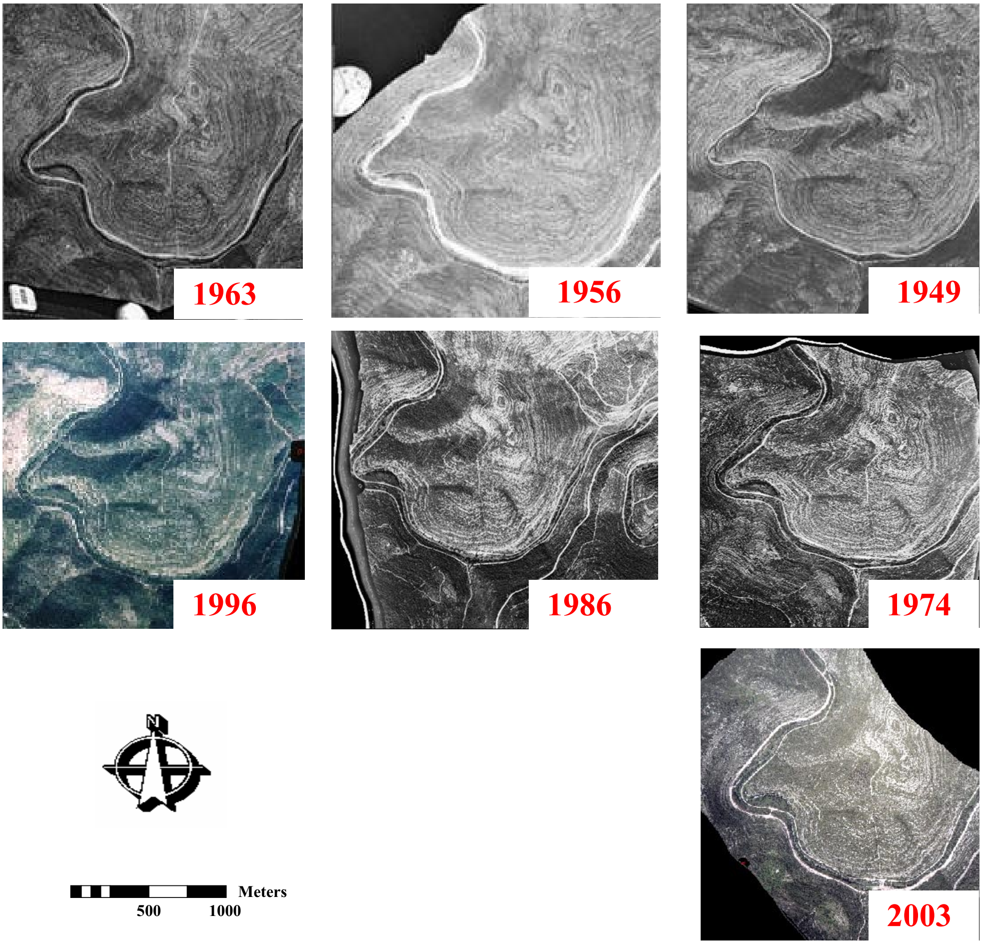

Figure 4. The seven orthophotos of the Mt Pithulim study site. The earlier ones (1949 to 1986) are panchromatic, the more recent ones (1996 and 2003) are in color.

### 4.3 *Gene flow patterns (parentage analysis)*

Parentage analysis can provide important insights to population spread (e.g. effective seed dispersal) and the genetic structure of populations. In order to characterize population spread from its earliest stages, we are currently concentrating our efforts in identifying and genotyping all individuals

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from the earliest generations established in the site. We screened ~130 individuals – presumably the oldest individuals in the site (though further examination is still needed) – using previously described and characterized microsatellites (SSRs) (Vendramin et al. 1996, Keys et al. 2000). Three chloroplast (paternally inherited) and four nuclear (biparentally inherited) SSRs were found to be variable and the five putative ancestors were found to have unique multilocus genotypes. For the parentage analysis we plan to use the software FaMoz (Gerber et al. 2003). [D. Troupin; in collaboration with G.G. Vendramin, CNR, Italy].

### 4.4 *Vegetation dynamics*

Reconstructing the history of spatial change in cover (vegetation) types during the study period (1940s to present) could help assess the role of biotic interactions in shaping pine expansion in the study site. We quantify this spatial change by analyzing recent and historical air photos (section 4.1). Five cover types were defined: adult pine trees, tall (> 2 m) woody species other than pines, shrubs and dwarf shrubs, annual herbs and exposed bedrock. We work on developing an automated procedure for classifying cover types in the recent and historical orthophotos, one for each decade. Classification procedures utilize a series of tools available through the ArcMap and ERDAS software packages, including illumination adjustment using kriging interpolation (a pre-classification phase), supervised classification and various other image processing tools. We shall apply several different classification schemes, and use fuzzy logic principles to generate the final map of cover types for each decade. The classification of the pine trees in all decades will be tested against the independently-derived mapping of pines (sections 3.3 and 4.1). The 2003 classification will be validated against a map resulting from a recent field survey. To test classification accuracy in previous decades, we shall use the ERDAS *Stereo Analyst* tool to classify cover type based on three-dimensional manual classification. [Y. Carmel & E. Namer, Technion; T. Svoray].

## 5 THE PRESENT: DEMOGRAPHIC AND GENETIC STRUCTURE

### 5.1 *Seed dispersal and seedling establishment*

A network of 94 large wooden-frame seed traps (total sampling area of 83 $m^2$) placed in 54 stations within the 60 ha plot has been established in the site in autumn 1996, and seed dispersal has been monitored weekly until summer 1998 (Nathan et al. 1999). We used these data to test the predictions of a dispersal simulation model (Nathan et al. 2001; section 6.2.1).

In winter 2002, we replaced this network by 172 plastic tub traps (total sampling area of 43 $m^2$). Seed traps are being checked every week during dispersal seasons and on monthly intervals in other periods of the year. Seeds collected from these traps will be used to test more detailed dispersal models (section 6.2.1), and for the analysis of gene flow patterns (section 4.3). [D. Troupin].

A network of 100 permanent plots is planned to be established in the site during the year 2004, to estimate the rates of seedling establishment and survival, and to elucidate their determinants, using both observational and manipulative experimental approaches. [O. Steinitz]

### 5.2 *Tree growth*

Tree ring data collected for age determination (section 4.2) are also used to examine tree growth and its determinants. A traditional analysis of this kind examines the correlation between ring width and large-scale factors such as annual precipitation and mean temperature that are typically averaged for areas of $10^8$ $m^2$ and more. However, the quantitative estimates of potentially influencing factors at much smaller scale of 100 $m^2$ and less provide a rare opportunity to examine the effect of local factors on tree growth as well.

We examined the correlations between ring width and multiple large- and small-scale factors for a sample of 48 trees within the 60 ha plot. Ring width is significantly negatively correlated with mean monthly maximum temperature of the previous year, and significantly positively correlated with annual precipitation of the current year, annual precipitation of the previous year, and Marchto-May precipitation of the current year. Among the small-scale factors, ring width was strongly positively correlated with the mean distance of a tree from its 4 nearest neighbors, and there was also a significant trend of decreasing ring width with increasing surface steepness. Residual analysis of the relative role of large vs. small scale factors revealed an overall more pronounced effect of the small-scale factors. [C. Bannai].

### 5.3 *Genetic structure and spatial autocorrelation*

Genetic structure, the clustering of like genotypes, has been described for many plant populations (Ennos 2001). We shall examine two of the main potential causes for the formation of a genetic structure: restricted seed dispersal and different levels of microhabitat adaptation in a heterogeneous environment. Using spatial autocorrelation methods, along with seed dispersal estimates obtained by a mechanistic model (section 6.2.1) and the spatial distribution of microhabitat conditions, the genetic structure formed in early stages of population spread will be examined. Preliminary results, obtained by using GenAlEx V5 software (Peakall and Smouse 2001), reveal the possible existence of a weak short-scale genetic structure. [D. Troupin; in collaboration with G.G. Vendramin].

## 6 THE FUTURE: MODELS OF POPULATION DYNAMICS

### 6.1 *Empirical (statistical) models*

Empirical models provide the means for a retroactive evaluation of spatial dynamics. Sites (grid cells of 5 x 5 m) in which trees had successfully established can be identified based on the reconstructed history of population expansion for each decade since the 1940s. Seed dispersal models (section 6.2.1) will be used to predict dispersal from adult trees of the previous decade, to estimate the seed-to-adult survival probability. We shall employ multiple regression methods to examine the correlation between this survival probability and various small-scale factors. [O. Steinitz].

### 6.2 *Mechanistic models*

By incorporating the key factors responsible for spatial change in plant population dynamics, mechanistic models can provide insights into the underlying mechanisms beyond those that can be obtained from empirical models. They can also provide a more adjustable tool to predict future changes for a diverse set of possible scenarios. We shall therefore concentrate our modeling efforts in developing mechanistic, rather than empirical, models of tree dynamics.

#### 6.2.1 *Seed dispersal models*

A simple mechanistic model of seed dispersal by wind (WINDISPER) has already been applied to the study site, revealing close agreement between predicted and observed seed densities in traps (Nathan et al. 2001). This model, however, does not describe turbulence in sufficient details. Therefore, it could be difficult to make adjustments for heterogeneous environments, in which structural changes can induce turbulent fluctuations that can strongly affect seed flight trajectories. We shall examine alternative atmospheric-ecological models of wind dispersal, e.g., a coupled Eulerian-Lagrangian simulation model, which has been developed, parameterized and tested for a temperate forest in North America (Nathan et al. 2002). This model describes the structure of turbulence within and above the canopy by using second-order moment closure techniques to estimate the Eulerian statistics of the wind field. These statistics, in turn, drive a stochastic Lagrangian simulation of seed flight in three-dimensional space. The biological parameters of this model are the leaf area density profile and the drag coefficient of the foliage, the vertical distribution of seed release height, and the seed terminal velocity. This model reliably predicted the vertical profile of seed dispersal, using a vertical array seed traps (Nathan et al. 2002). The model is relatively simple, does not require highly specialized measurements for calibration and can run quite fast on a standard computer, hence its great potential as a general tool for modeling wind dispersal.

### 6.2.2 *Demographic models*

Matrix population models (Caswell 2000) provide useful tools to incorporate age- or stage-specific variation in demographic parameters, features that characterize the process of plant recruitment. These models are also compelling since they facilitate a data-modeling approach of estimating stage transitions from field data, and because they directly lend themselves to sensitivity analysis of the factors that determine recruitment and population growth. Habitat effects, for example, can be examined by comparing transitions estimated from data collected at different habitats. The matrix population model for Aleppo pine population on Mt Pithulim will include the following six stage classes: seeds, seedlings (2 years), saplings (3-6 years; non-reproductive), and small (<50 mm DBH), medium (50-100 mm DBH), and large (>100 mm DBH) reproductive individuals (ranges are based on measurements of 243 juvenile trees in a native population on Mt Carmel).

### 6.2.3 *Spread models*

A general modeling framework, recently proposed by Neubert and Caswell (2000), provides the means to examine the role of specific demographic stages on spatial spread by coupling stage-specific demography (by matrix population models) with dispersal (by integrodifference equations). However, their simplifying assumption of spatial homogeneity in dispersal and establishment must be relaxed to realistically describe spatial spread. This will be achieved by (1) replacing the phenomenological dispersal model currently applied in this framework with mechanistic ones (6.2.1); this would be the first attempt to combine matrix models with mechanistic dispersal models, and (2) incorporating spatial variation in the transition probabilities describing the establishment process (6.2.2). The spread model will describe the spatially-explicit dynamics of individual trees (dispersed seeds to reproductive adults), incorporating stochasticity in their growth, reproduction and death in discrete time steps. [O. Steinitz].

An alternative approach has been developed using fuzzy logic principles (Svoray and Nathan 2003). In this model, seed dispersal is simulated by WINDISPER (section 6.2.1); seed survival increases with distance from adult trees due to attraction of seed predators to areas of high seed densities near adults; germination is affected by rainfall, temperature, wetness and slope orientation; and seedling survival to maturity increases with distance from adult trees due to attraction of seedling herbivores to areas of high seedling densities near adults. The four main stages (seed dispersal, seed survival, germination and seedling survival) were given equal weights in calculating the joint membership function. A preliminary analysis using 80 of the oldest trees revealed a significant tendency of trees to be located in cells predicted to hold high potential for recruitment, whereas trees tend to be absent from cells of low potential for recruitment (Svoray and Nathan 2003).

## 7 CONCLUSIONS

The main goal of this ongoing research is to investigate the mechanisms of spatial spread in tree populations. Towards this end, this project develops an integrated theoretical-empirical framework that utilizes a diverse set of methodological tools and encompasses multiple processes affecting spatial population dynamics of trees in a heterogeneous environment. This research is expected to make both theoretical and applied contributions to plant dynamics research. It will shed light on the mechanisms of spatial spread in plant populations. To the best of our knowledge, this is the first comprehensive attempt to quantify, analyze and evaluate the biotic and abiotic factors that jointly determine the spread of any tree population. In an applied context, it should provide a powerful new tool to describe and predict population spread of trees for management purposes. Specifically, the proposed research has practical implications for predicting (1) tree expansion for the management of natural and planted forests, (2) natural regeneration for the planning of sustainable afforestation and reforestation projects, (3) spatial population dynamics in fragmented landscape, and (4) range changes in response to future climate change. Since forests are important atmospheric carbon sinks, and since wind-dispersed species are important components of many forest ecosystems, predicting the expansion of wind-dispersed trees is of global significance.

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