PRINCIPAL ABIOTIC FACTORS INFLUENCING THE STRUCTURE AND FUNCTION OF MATURE PINE FORESTS IN ISRAEL

A Thesis

by

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ABSTRACT

Mediterranean forests are water limited. While understanding that the growth and survival of these systems are strongly influenced by water availability, the interactive effects of precipitation and other edaphic and topographic factors on forest performance and the importance of these environmental abiotic factors in light of heavy human influence is less clear. The purpose of this project was to (1) assess how abiotic factors such as precipitation, elevation, bedrock and aspect affect the structure and function of Israel's mature (> 30 years) *Pinus halepensis* and *Pinus brutia* forests, (2) determine whether the growth and performance of both species was different in response to abiotic factors and (3) assess how abiotic factors and overstory canopy coverage influence understory growth and development. Inventory data of ninety-six *P. halepensis* and seventy-four *P. brutia* stands were analyzed that were planted throughout Israel. Tree growth such as height, stem diameter, and mean basal area increment and stand-level characteristics such as stem density, basal area, and Landsat NDVI were analyzed. In addition, understory volume data such as total, pine, and oak volume, was collected and analyzed from a subset of the same stands, specifically forty-eight *P. halepensis* and thirty-two *P. brutia* stands.

Stepwise multiple linear regression models were produced. For *P. halepensis,* precipitation was the determining factor influencing forest performance for all models produced (40 - 92% of explained variation) with an additional positive influence of north vs. south facing aspects, while for *P. brutia* forests the results were more complicated, as interacting effects between the four abiotic factors were prevalent, mostly aspect × elevation for individual tree characteristics and precipitation × bedrock for stand-level ones. No conclusive explanation was found that would account for these discrepancies, but temperature limitation, or possibly management, might have important contributing effects. Understory development in both forests was positively related to precipitation, while overstory canopy coverage had a minimal effect. The conclusions of this study highlight the need to consider site-specific water based management regimes. In addition, future management decisions should account for the sensitivity to changes in water availability for both species, and temperature for *P. brutia.*

DEDICATION

To my wife, Misti

It is to her credit I was able to complete this work. May we enjoy the fruits of these labors for many years to come.

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NOMENCLATURE

AAP	Average Annual Precipitation
A.S.L.	Above Sea Level
BA	Basal Area
C	Celsius
CM	Centimeters
DBH	Stem Diameter at 4.5 feet
GIS	Geographic Information Systems
HA	Hectare
KKL	Israel Forest Service Keren Kayemeth LeIsrael
LTM	Long Term Monitoring
LTFMP	Long Term Forest Monitoring Program
MBAI	Mean basal area increment
M	Meters
MM	Millimeters
NDVI	Normalized Difference Vegetation Index
NIR	Near Infrared Region
P.	Pinus
RED	Reflectivity in the Red Region
TPH	Trees Per Hectare
UWV	Understory Woody Vegetation
VIF	Variance Inflation Factor
YR	Year

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CHAPTER I

INTRODUCTION

Pine forests exist throughout the Mediterranean across a wide environmental gradient occurring from sea level into mountainous regions. Growing in dry sub-humid to semi-arid environments, the extent of these forests is presumed to be strongly affected by water availability. In addition, human influences (e.g. agriculture, livestock grazing) have exerted a strong control on forest extent throughout the region (Biondel 2016; Scarascia-Mugnozza et al. 2000; Tomaselli 1977). In contrast, a concerted tree planting effort has occurred in Israel over the last century, resulting in man-made monocultures of mainly conifer species (Ginsberg 2000). Planted across a wide range of climate and bedrock types, it is unclear how these species have responded in growth and regeneration across the region, making it difficult to develop adequate plans for the sustainable management of these forests (Osem et al. 2008).

The pine forests in Israel were established by the Jewish National Fund (hereafter referred to as KKL), a non-governmental organization that acts as the Israel forest service, starting in 1908 (Ginsberg 2000). In total, the KKL has established nearly 100,000 ha of planted forests (60% pine forests), of which 85,000 ha were planted during the last 60 years (Figure 1). While three coniferous species were mainly planted – Aleppo pine (*Pinus halepensis* Mill.), Brutia pine (*Pinus brutia* Ten.) and the Common cypress (*Cupressus sempervirens* L.), the native Aleppo pine was the dominant one, covering nearly 40% of the forested area (Osem et al. 2008).

The major objectives of afforestation in Israel during the 1920s – 1970s were to reclaim and protect eroded hillsides, provide employment, and improve the landscape to encourage settlement (Amir and Rechtman, 2006). In addition, wood production was seen as an important by-product of afforestation (Bonneh 2000) and provided an impetus to maximize forest productivity through management (Gindel 1952; Perevolotsky and Sheffer 2009; Osem et al. 2008). Thus, high planting densities and seven-year thinning cycles were implemented across the forested region (Bonneh 2000). However, by 1965 it had become clear that wood production would not be economically feasible due to poor growth rates and inferior wood quality (Saltiel 1965). While the timber-themed management strategy was successful in achieving its initial objectives, the KKL had to gradually shift its main effort towards forest maintenance as new areas for afforestation were exhausted. Moreover, difficulties in the maintenance of these manmade forests began to rise as they developed. For example a major pest outbreak by the Israeli pine bast scale, *Matsucoccus josephi* Bodenheimer et Harpaz (Matsucoccidae), caused massive mortality in Aleppo pine stands during the 1970 - 1990s (Perevolotsky and Sheffer 2009; Bonneh 2000). In light of this, the KKL reduced the number of Aleppo pine plantings in exchange for the exotic Brutia pine, which was not affected by the pine bast scale (Mendel 2000; Bonneh 2000). As the KKL strives to promote the continued vitality of the current and future state of these forests, manager focus has turned towards understanding how these forests have been influenced by the climatic and edaphic conditions under which they have developed. It should be noted that some of these forests were planted well beyond their native range.

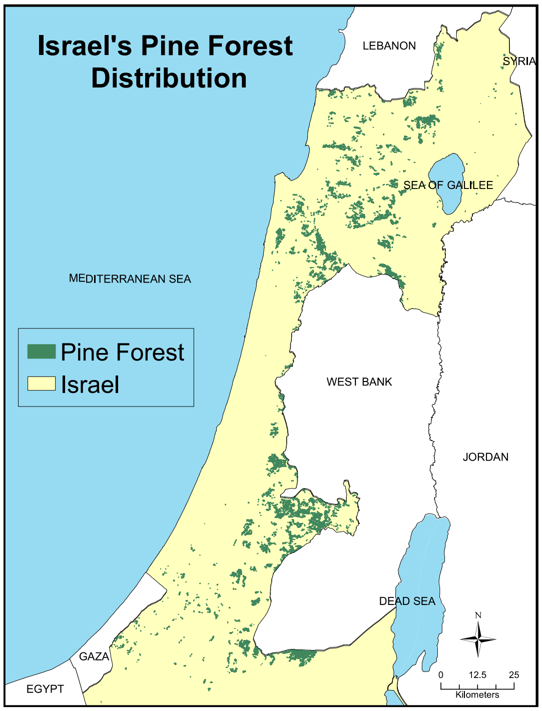

Figure 1. Distribution of Israel’s pine forests.

Israel’s monoculture even-aged pine forests are in contrast to the once widespread native Mediterranean dwarf shrublands and dense woodlands (Rabinowitch 1985). Although highly degraded and over grazed at the beginning of the 20th century, the regeneration of these native broadleaf species has occurred in the understory of many established pine forests. However, the distribution and composition varies across environmental gradients (Osem et al. 2009), grazing levels and topography (Carmel and Kadmon 1999), and presumably overstory coverage, as this affects understory development as sun-light becomes a limiting resource. As many of Israel’s forests are nearing the end of their life expectancy, the focus of forest managers is gradually turning towards long-term management for forest regeneration (Osem et al. 2008). Therefore it is becoming increasingly important to develop an understanding of how the forests' overstory and understory vegetation interact and develop in relation to environmental conditions, species selection (*P. halepensis* and *P. brutia*), and stand characteristics, such as stand density, that affect resource availability and regeneration.

Stand density refers to the degree of crowding of stems within a forest area (Ginrich 1967) and is most commonly measured using two indices; number of trees and basal area per unit area (Hyink and Zedaker 1987). Abiotic factors interact with stand density to affect individual tree growth, viability, and the regeneration potential of tree and understory species. In even-aged monoculture forests the amount of available growing space (resources) per tree decreases as stand density increases, possibly causing stress among individual trees. In the absence of disturbance, natural mortality (self-thinning) occurs in maturing forests resulting from an increase in tree size and decrease in self-tolerance (Zeide 1991; Hyink and Zedaker 1987; Oliver and Larson 1996), with upper limits for tree occupancy quantified for a number of species (Reineke 1933; Yoda 1963). When high densities are maintained in a forest the potential increases for a pathogen to kill trees in excess of self-thinning, and this potential increases further when the trees are under abiotic stress. Initial planting of both pines in Israel were initially done at high densities (Bonneh 2000). Subsequent thinning and lower planting densities were employed as it became clear that drought stress and pathogens posed a threat to the survival of overly dense forests.

Currently the KKL faces the challenge of developing a forest management strategy that will take into account the variability in habitat condition and promote the vitality of the current forest generation (planted forest) while ensuring the regeneration and development of the next forest generation as a sustainable, ‘multifunctional’ forest (Osem et al. 2008, 2009). Improved understanding is needed of how principal environmental factors interact in determining pine forest structure and function and the regeneration and development of understory vegetation. Israel’s mature (> 40yrs old) *P. halepensis* and *P. brutia* forests were established within a limited time frame using a fairly uniform management strategy (e.g. site preparation, planting density, thinning regime), provide a unique opportunity to study the way by which principal abiotic environmental factors interplay to determine pine forest structure and function.

The purpose of this study was to provide a comprehensive examination of how environmental factors interact to affect the forest structure and function of mature pine plantations in Israel. A thorough examination of forest growth and performance was carried out using the inventory database of KKL. In addition, a ground survey looking at understory development was implemented and satellite imagery (Landsat) was used to assess ecosystem characteristics at larger scales. This is the first comprehensive study of the intraspecific variation within mature Israeli Pine forests at a country-wide scale, and across the environmental factors assumed to be the main determinants of forest performance in this region. The study focused on the following principal environmental factors including their interactions:

1) Precipitation amount
2) Bedrock type
3) Topographic aspect
4) Elevation

This research will help forest managers develop conservation and regeneration strategies for Israel's future forests. This study will also contribute to the development and assessment of the various parameters describing forest structure and function, potentially improving an understanding of how climate change will affect these forests as well as similar conifer forests of the western and southern Mediterranean.

CHAPTER II

ABIOTIC FACTORS INFLUENCING THE STRUCTURE AND FUNCTION OF ISRAEL’S MATURE PINE FORESTS

II.1 HYPOTHESES, RATIONALE, AND ASSUMPTIONS

In assessing the impact that abiotic factors have had on mature pine forest structure and function three hypotheses have been developed. These hypotheses are meant to test the current understanding of this system, enabling this project to offer alternative hypotheses that may prove helpful for the future management of these systems.

II.1.1 Hypothesis 1

H1a: Precipitation amount and elevation positively affect forest performance.
H1b: Forest stands growing on soft bedrock outperform those growing on hard bedrock and stands growing on north facing aspects outperform those growing on south facing aspects.
H1c: Among these abiotic factors, precipitation amount is the primary environmental factor determining forest performance.

Rationale: Plant productivity in this Mediterranean region is generally considered water limited (Pigott and Pigott 1993). As mature forests are assumed to have reached a state of ecohydrological equilibrium with their environment, it is expected that the studied abiotic environmental variables would have influenced past forest performance mainly through their effects on water balance. Precipitation amount is considered to be the primary factor influencing forest performance in water limited systems. Other environmental factors are also assumed to influence water availability with elevation and topographic aspect influencing evapotranspiration rate through air temperature and sun radiation load, and bedrock type influencing water holding capacity in the root zone. While the individual effect on water availability of these additional environmental factors are perceived to be known, uncertainty exists regarding the extent of their influence and relative importance and interaction patterns along precipitation gradients. In addition the studied forests have developed under a strong human influence making it uncertain to what extent forest structure has actually been determined by abiotic factors. The following outlines the multiple linear regression and hypotheses that I will test in my thesis.

Equation:

$$Y = \beta_0 + \sum_i \beta_i \mathcal{X}_i + \sum_{ij} \beta_{ij} \mathcal{X}_{ij} + \epsilon$$

Hypotheses:

$$H_1 : \beta_{1(Precipitation)} > 0$$

$$H_2 : \beta_{2(Elevation)} > 0$$

$$H_3 : \beta_{3.1(Bedrock.Hard)} < \beta_{3.2(Bedrock.Soft)}$$

$$H_4 : \beta_{4.1(Aspect.South)} < \beta_{4.2(Aspect.North)}$$

$$H_5 : \beta_{ij\ldots} \neq 0$$

II.1.2 Hypothesis 2

H2: *P. halepensis* and *P. brutia* responses to abiotic environmental factors are similar.

Rationale: *P. brutia* and *P. halepensis* are taxonomically similar species and traditional forest management has treated these two species in the same manner. However, unlike *P. halepensis*, *P. brutia* was established outside its native range and consideration was given to the lower level of drought tolerance *P. brutia* vs. *P. halpensis* (Bonneh 2000). Still, it is unclear whether the growth and performance of both species is different in response to abiotic factors.

Equation:

$$Y = \beta_0 + \sum_i \beta_i \mathcal{X}_i + \sum_{ij} \beta_{ij} \mathcal{X}_{ij} + \epsilon$$

Hypothesis:

$$H_0 : \beta_{i(P.halepensis)} = \beta_{j(P.brutia)}$$

II.1.3 Hypothesis 3

H3: Understory development is positively related to increasing precipitation up to a point at which light availability, as indexed by overstory basal area, becomes the main limiting factor for understory development.

Rationale: Understory development in Mediterranean coniferous forests has been shown to increase with increasing water-availability (Osem 2011) and decrease under higher canopy coverage (Jennings 1999). However similar to the overstory relationship to precipitation, additional abiotic environmental factors (e.g. bedrock and elevation) may also influence understory development as these factors affect plant water balance. I assume the following relationships to understory development will be evident despite the high levels of disturbance by human influences (e.g. grazing and recreation).

Equation:

$$Y = \beta_0 + \sum_i \beta_i \mathcal{X}_{\square} + \sum_{ij} \beta_{ij} \mathcal{X}_{ij} + \epsilon$$

Hypotheses:

$$H_1 : \beta_{1(Precipitation)} > 0$$

$$H_2 : \beta_{2(Elevation)} > 0$$

$$H_3 : \beta_{3.1(Bedrock.Hard)} < \beta_{3.2(Bedrock.Soft)}$$

$$H_4 : \beta_{4.1(Aspect.South)} < \beta_{4.2(Aspect.North)}$$

$$H_5 : \beta_{5(Basal\ Area)} > at\ some\ threshold$$

$$H_6 : \beta_{ij\ldots} \neq 0$$

II.2 LITERATURE REVIEW

II.2.1 Abiotic Influences on Forest Performance

Understanding the influence of various abiotic factors on forest structure and function has always been a challenge of major silvicultural importance. Such an understanding is necessary in forestry to understand how various management goals may be achieved under varying climatic and edaphic conditions. A good example of a management goal which requires such an understanding would be the conservation of forests under ongoing climate change and increasing drought stress. This is particularly challenging in first generation manmade forests established across highly variable habitat conditions, some of which developed beyond the natural forest range and under high human impact. These are characteristics of Israel's planted coniferous forests (Osem et al. 2008).

Some influences of environmental factors on forest structure and function are well known and accepted. For instance, it is commonly accepted that Mediterranean systems are water limited and their performance is thus strongly related to precipitation amount (Pigott and Pigott 1993; Peñuelas et al. 2001, Sabaté et al. 2002; Hoff and Rambal 2003). Nevertheless, it has been suggested that even this fundamental relationship may only be evident up to a certain precipitation level (i.e., ca 600 mm yr^{-1}, Rabinowitch, 1985) above which other environmental factors, such as bedrock type and soil mineral composition, may become more important. Additionally, it has been shown that the effects of drought episodes on forest performance may vary across climatic gradients (Allen et al. 2010; Babst et al. 2013; Linares et al. 2009). Furthermore, it has been shown that environmental factors, other than precipitation, may strongly affect water availability. For instance, north-facing slopes exhibit more developed vegetation density than south facing slopes in water limited systems, with this phenomenon being attributed to differences in sun radiation flux and resulting evapotranspiration rate (Carmel and Kadmon, 1999; Sternberg and Shoshany, 2001; Coble et al. 2001). Even the rate of resin flow from *P. halepensis* was shown to be influenced by topographic aspect, where trees on north facing slopes have exuded more resin than those on south facing ones (Zamski 1970).

Other studies in Israel have emphasized the importance of bedrock type as a major environmental factor influencing forest performance. For example, Heth (1969) found *P. brutia* forests to be significantly influenced by bedrock. The species was more prevalent on soft bedrock than hard bedrock, likely because more frequent fissures allowed tree roots to penetrate into bedrock layers. Heth also found tree growth was more negatively affected by solar radiation on south facing aspects vs. northern aspects. The importance of bedrock and aspect along a precipitation gradient was further highlighted by Schiller (1982) in determining the performance of *P. halepensis* forests. Here topographic aspect showed only a minor influence on tree performance in a region with relatively high precipitation (ca 630 mm yr^{-1}) and a more pronounced influence in a region with lower precipitation (ca 300 mm yr-^{1}). In addition, lower levels of stand performance were found on hard vs. soft bedrock. Similarly, topographic aspect along a precipitation gradient also affected tree performance during drought, where trees in arid regions (<350 mm rainfall yr^{-1}) were more negatively affected by the drought than those in more humid areas (>500 mm rainfall yr^{-1}, Dorman et al. 2013a). Others studies have highlighted the negative effects on *P. halepensis* caused by shallow soils and hard bedrock and emphasized that the hardness of rocks has a greater influence on the performance of trees than all other site factors (Heth 1965; Schiller 1972; Seligman and Douer 1971).

The influence of precipitation combined with elevation/temperature has been emphasized as an important driver of forest growth based on dendrochronological studies. For example, Lev Yadun et al. (1981), using the oldest *P. halepensis* trees in Jerusalem, found growth rates to be sensitive to precipitation and temperature, where high precipitation combined with low maximum temperatures in the spring (starting in March - May) showed the best growth responses. A similar response was also seen in France (Serre 1976). Sarris et al. (2007) found *P. halepensis* and *P. brutia* growth rates in the Samos Island of Turkey to be influenced by annual precipitation with even higher correlations using two year analysis, raising the importance of multiyear precipitation impacts. Similarly, other native species in Israel were found positively influenced by precipitation and temperature (Fahn et al. 1963; Liphschitz and Waisel 1967).

Although several studies in Israel and the Mediterranean region have already dealt with the effects of water related environmental conditions on the performance of pine plantations, major gaps in understanding still remain (Scarascia-Mugnozza et al. 2000). This is partly because many studies were limited in the extent of both the environmental variables studied and the measured forest performance parameters. A more comprehensive approach that takes into account a larger variety of relevant environmental factors, including their interactions, and examines their influences on a variety of parameters describing forest structure and function in both *P. halepensis* and *P. brutia*, such as this project intends to do, will promote our understanding regarding the performance of pine forests in the East Mediterranean, Israel.

II.2.2 Differences in Species Response

While *P. halepensis* and *P. brutia* are taxonomically close, differences exist in their water requirements for growth and survival. According to Schiller (2000) and Quézel (2000), *P. brutia*, an eastern Mediterranean pine species not native to Israel, grows in the semi-arid and subhumid bioclimates where precipitation is greater than 400 mm yr^{-1}. *P. halepensis* is mostly a western Mediterranean pine species but native to eastern Mediterranean Israel and across the Mediterranean to Spain and Morocco. This species is considered less sensitive in its water requirements and grows in the arid, semi-arid, and sub-humid bioclimates where precipitation is greater than 250 mm yr^{-1}. Genetic differences do exist between the eastern and western *P. halepensis* ecotypes as eastern ecotypes (Greece, Israel) were found to be more drought resistant than the western ecotypes (Schiller 2000).

Edaphic and altitudinal requirements for *P. halepensis* and *P. brutia* are similar. Both species occur in the thermo-Mediterranean and meso-Mediterranean zones where average annual temperatures are 13°C to more than 20°C, and elevation gradients from sea level to high altitudes (e.g., maximum 1500m and 2000m for *P. halepensis* and *P. brutia* respectively, Quézel 2000). Both species grow naturally on a variety of soil and bedrock types but neither species tolerates poorly drained soils (Quézel 2000). *P. halepensis* favors soft calcareous bedrock as chalk and marls but can also grow well on hard limestone and dolomite. Thus, it can be found on terra rossa and dark to bright rendzina soils (Quézel 2000; Schiller 1982). Similarly, *P. brutia* favors soft bedrock and rendzina soils (Boydak 2004).

In effect, it has been well established that *P. brutia* is more sensitive than *P. halepensis* to unfavorable ecological properties, such as high insolation (exposure), hard bedrock and shallow soils (e.g., low soil water availability, Heth 1965, 1969; Oppenheimer 1967; Waisel 1959). *P. halepensis* is more resilient in its ability to penetrate deep into bedrock and other rock crevices (Oppenheimer 1955, 1957, 1967) and has a greater ability to induce dormancy in the upper root system (Leshem 1965, 1967) than *P. brutia* (Waisel 1959), which provides some protection against drought. Despite a fairly good understanding of how abiotic stress factors generally affect both species, uncertainty remains in knowing how the growth and performance of these species are related to abiotic environmental conditions interacting with management schemes (e.g., stand density) to affect the viability and regeneration potential of these forests.

II.2.3 Understory Woody Development

Several studies in Israel and the Mediterranean have investigated the influence of environmental factors on understory development. A study conducted across the entire precipitation gradient within the Mediterranean zone of Israel found that understory woody vegetation (UWV) development and regeneration of native broadleaved trees were positively related to precipitation with an additional positive effect on north facing aspects when compared to south facing aspects (Osem et al. 2009, 2011). This study, however, showed no relationship between precipitation and pine regeneration and did not account for differences in bedrock or elevation**.** Similarly, a study in Mediterranean Spain conducted a large-scale assessment of plant regeneration and diversity in plantations over a wide environmental range including variation in precipitation, elevation, and topographic aspect. Pronounced variation in regeneration and plant diversity were found in plantation understories along the gradients examined, though the importance of silvicultural history was also highlighted (Gómez-aparicio et al. 2009).

The relationship between UWV and abiotic factors are complicated (Osem et al. 2011). Interactions between other factors such as silvicultural strategy and history (Maestre and Cortina 2004; Takafumi and Hiura 2009; Navarro et al. 2010), overstory characteristics (Barbier et al. 2008; Coll et al. 2010; Gomez-Aparicio et al. 2009), sun light availability (Jennings et al. 1999; Rodríguez-Calcerrada et al. 2008), and competing herbaceous vegetation (Hibsher et al. 2013; Koukoura and Kyriazopoulos 2007) all have competing and facultative effects on UWV.

II.3 MATERIALS AND METHODS

II.3.1 Regional Characteristics

Israel’s pine forests were planted on non-arable hillsides and mountains in the Mediterranean zone (northern half) of Israel, in areas receiving 250 to 900 mm of annual precipitation (Orni and Efrat 1980). These forests were planted on shallow and stony soils that were often not more than a few centimeters in depth (Figure 2). Prevalent soil and bedrock types include terra rosa and rendzina (Schiller 2000) and soft (chalk-marl) and hard (limestone-dolomite) calcareous bedrock (Schiller 1982; Rabinowitch 1985). Topographically most forests are located in mountains regions and along the upper coastal plains ranging in elevation from 40 to 900 m a.s.l.. The climate is characterized as east Mediterranean with hot dry summers and cool moist winters occurring mainly during December through March with a majority of annual precipitation falling during winter (Osem et al. 2009). Average monthly temperatures vary during winter from 4.5 to 10 °C and 19 - 30 °C during summer months (Kafle and Bruins 2009).

II.3.2 Native Vegetation

Native Mediterranean vegetation is composed of dense woodlands, known as maquis, of *Quercus calliprinos* Webb. and *Pistacia palaestina* Boiss in the more humid mountainous regions, shrublands and sparse woodlands of *Ceratonia siliqua* L., *Pistacia lentiscus* L., *Quercus itahaburensis* Decne. and *Styrax offinalis* L. in lower, drier regions of the country and dwarf shrublands of mainly *Sarcopoterium spinosum* in the semiarid transition zone (Bonneh, 2000). *P. halepensis* is the only pine species native to Israel and during the previous century was restricted to a few small remnant populations in the Carmel, Galilee and Judean mountainous regions (Weinstein-Evron and Lev-Yadun 2000). Degradation of these natural woodlands occurred for centuries due to over exploitation of forest resources, livestock grazing and the devastation of forests through wars resulting in a landscape denuded of trees by the early 1900s (Kadmon & Harari-Kremer, 1999; Tomaselli, 1977).

II.3.3 Data Set

This project analyzed two datasets that reflected a survey of 170 stands designated as part of Israel's long term forest monitoring program (LTFMP, Sprintzin et al. 2014). The first dataset, hereafter referred to as overstory dataset, consisted of current inventory data from each stand, measured prior to the establishment of the LTFMP by KKL field crews, compiled into a singular dataset. This inventory dataset was collected from 2000 - 2012 and consisted of averaged overstory tree height, stem diameter, density, and basal area measured in randomly distributed 8 m radius plots in each stand (sampling effort of ca. 5%).

Figure 2. Example of *Pinus halepensis* tree growing on top of the bedrock layers (A) and in shallow soils (B) in Israel.

In addition, stand basal area (BA) and tree BA increment were calculated using stem diameter measurements. Mean basal area increment (MBAI), an index of tree growth rate, is defined as:

$$\text{MBAI (cm}^2\text{ y}^{-1}) = \frac{\pi r^2}{age}$$

where r is stem radius (cm) at breast height. Finally, remote sensing data (normalized difference vegetation index (NDVI)) for the same set of forest stands was extracted from Dorman et al. (2013a, 2013b) and added as an additional variable. NDVI is the most common remote sensing index in ecological studies (Dorman 2013a) and in this study was used as a measure of forest performance. NDVI values collected over a five year period (2006 - 2009 and 2011, 2010 data was not available due to heavy cloud cover) were averaged and included as an additional overstory variable. NDVI was calculated as:

$$\text{NDVI} = (\text{NIR} - \text{RED})/(\text{NIR} + \text{RED})$$

where NIR is the reflectivity in the near-infrared region (Landsat band 4) and RED is the reflectivity in the red region (Landsat band 3) of the electromagnetic spectrum. Further information regarding image pre-processing can be found in Dorman et al. (2013a, 2013b).

The second dataset, hereby referred to as the understory dataset, consisted of understory and overstory canopy coverage data measured for eighty of the one hundred and seventy forest stands during 2014 and 2015 as part of the first series of LTM plot establishment **(**Figure 3). At each stand a 40 × 120 m rectangular plot, consisting of four circular subplots (8 m radius each) with a 16 m transect running inside the length of each subplot, was established in a representative area of the stand. In each subplot, UWV was measured along the transect using the point-intercept method (Jonasson 1988) with 33 points being sampled at every half meter with the presence and height of vegetation, according to species, being recorded at each point. In addition, basal area was measured at each subplot to assess overstory canopy coverage. UWV volume was then calculated by (1) surface cover - the proportion of the transect covered by vegetation; (2) average height (weighted by cover); and (3) specific volume - the product of surface cover [proportion] × area [m^2] × average height, resulting in m^3/m^2 (Osem et al. 2011).

II.3.4 Research Plot Setup

The research plots (LTFMP) were randomly selected by stratifying Israel's *P. halepensis* and *P. brutia* mature (≥ 40 years) pure (> 70% of overstory trees) forests through categories defined for annual precipitation amount (250-400 mm, 400-600 mm, above 600 mm), bedrock type (hard calcareous, soft calcareous), elevation (above or below 400 m a.s.l.), and topographic aspect (North or South). Thus, 48 combinations were possible (Table 1). ArcGIS 9.3 (ESRI, 2009) was employed to select a stratified random set of stands with seven plot

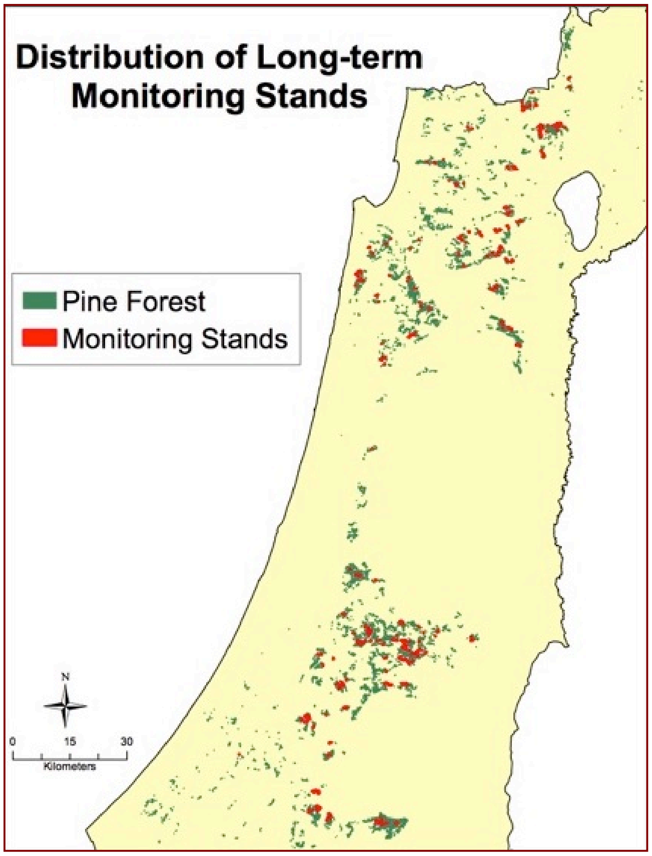

Figure 3. Distribution of Israel's pine forest and stands selected as part of the long-term forest monitoring program. Monitoring stand layer (red) has been enlarged for illustration.

replicates. As *P. brutia* was not planted in the low rainfall level, and some combinations had less than seven replicates, 170 stands were selected as sites for permanent monitoring

Plot listings were generated using the Israeli Forest Service's geographic information system layers wherein the precipitation layer was compiled from historically averaged data from the Israeli Meteorological Service, elevation and aspect layers were based on a digital elevation model, wherein stands were classified as north when falling within 315-0° and 0-45° or south when falling within 135-180° and 180-225°. The bedrock layer was estimated from a GIS layer that had been created from the digitization of 1:50,000 geological maps (Geological Survey of Israel).

II.3.5 Statistical Analysis

Stepwise multiple regression analyses were performed to test the stated hypotheses. Stepwise regression controls were set using a mixed-selection technique with p-value threshold of 0.1 to determine the model providing the "best" prediction of environmental variables and their interactions. Separate and joint analyses were performed on the overstory datasets for *P. halepensis* and *P. brutia*. The procedure was then repeated for the understory dataset.

The overstory dataset consisted of six dependent variables - height, diameter, density, basal area, MBAI, and NDVI, while the understory dataset consisted of three dependent biovolume variables - total, pine, and oak. Independent variables were environmental variables (precipitation, elevation, bedrock, and slope aspect). Precipitation and elevation were analyzed as continuous variables while topographic aspect and bedrock type were analyzed as nominal variables. As MBAI is an integrated estimate of tree growth, which is directly influenced by forest density, density was added to the MBAI model as a covariate to account for the density effect on individual tree growth. Stand age was added as a covariate to all models, except the MBAI model, to account for the variation in forest age. This analysis did not consider the age × abiotic factors interactions, nor the basal area × abiotic factor interactions in the understory dataset analysis, rather only the abiotic factor × abiotic factor interactions (e.g., precipitation × aspect). Consideration for the age × abiotic factors

Table 1. Environmental combinations and associated status in the Israel forest landscape. Precipitation and elevation categories are defined as follows: Precipitation - Low = 250 - 400 mm, Med = 400 - 600 mm, High = >600 mm; Elevation - Low = below 400 m, High = above 400 m.

Species	**Precip.**	**Bedrock**	**Aspect**	**Elev.**	**Status**	**Species**	**Precip.**	**Bedrock**	**Aspect**	**Elev.**	**Status**
P.halepensis	Low	Hard	North	Low	Exist	*P.brutia*	Low	Hard	North	Low	NA
P.halepensis	Low	Hard	North	High	NA	*P.brutia*	Low	Hard	North	High	NA
P.halepensis	Low	Hard	South	Low	Exist	*P.brutia*	Low	Hard	South	Low	NA
P.halepensis	Low	Hard	South	High	Exist	*P.brutia*	Low	Hard	South	High	NA
P.halepensis	Low	Soft	North	Low	Exist	*P.brutia*	Low	Soft	North	Low	NA
P.halepensis	Low	Soft	North	High	Exist	*P.brutia*	Low	Soft	North	High	NA
P.halepensis	Low	Soft	South	Low	Exist	*P.brutia*	Low	Soft	South	Low	NA
P.halepensis	Low	Soft	South	High	Exist	*P.brutia*	Low	Soft	South	High	NA
P.halepensis	Med	Hard	North	Low	Exist	*P.brutia*	Med	Hard	North	Low	Exist
P.halepensis	Med	Hard	North	High	Exist	*P.brutia*	Med	Hard	North	High	Exist
P.halepensis	Med	Hard	South	Low	Exist	*P.brutia*	Med	Hard	South	Low	Exist
P.halepensis	Med	Hard	South	High	Exist	*P.brutia*	Med	Hard	South	High	Exist
P.halepensis	Med	Soft	North	Low	Exist	*P.brutia*	Med	Soft	North	Low	Exist
P.halepensis	Med	Soft	North	High	Exist	*P.brutia*	Med	Soft	North	High	Exist
P.halepensis	Med	Soft	South	Low	Exist	*P.brutia*	Med	Soft	South	Low	Exist
P.halepensis	Med	Soft	South	High	NA	*P.brutia*	Med	Soft	South	High	Exist
P.halepensis	High	Hard	North	Low	Exist	*P.brutia*	High	Hard	North	Low	Exist
P.halepensis	High	Hard	North	High	Exist	*P.brutia*	High	Hard	North	High	Exist
P.halepensis	High	Hard	South	Low	Exist	*P.brutia*	High	Hard	South	Low	Exist
P.halepensis	High	Hard	South	High	Exist	*P.brutia*	High	Hard	South	High	Exist
P.halepensis	High	Soft	North	Low	Exist	*P.brutia*	High	Soft	North	Low	Exist
P.halepensis	High	Soft	North	High	Exist	*P.brutia*	High	Soft	North	High	Exist
P.halepensis	High	Soft	South	Low	Exist	*P.brutia*	High	Soft	South	Low	Exist
P.halepensis	High	Soft	South	Low	Exist	*P.brutia*	High	Soft	South	Low	Exist

interactions and the basal area × abiotic factor interactions will be given in the forthcoming journal publication of this work.

Overstory canopy coverage was hypothesized to directly influence understory development, therefore overstory BA was used as a covariate to the analyses of understory volume variables. Final models were then produced for all dependent variables after removing any outliers upon extracting the studentized residuals and removing any values greater than ± 3 (Cook 1977). Level of significance was set at 0.05 and all analyses were performed using JMP Pro 12.0 (SAS Institute, Cary, NC, US).

Normal distribution of error was checked using the Shapiro-Wilks W test. Homogeneity of variances was checked visually by examining residual and predicted values of the model. Data lacking normal distribution and/or homogeneity of variances was mathematically transformed to meet these assumptions. As understory volumes failed to meet the assumptions of normality even after common transformations were employed, rank averaged transformation was used (Conover & Iman, 1981). Multicollinearity between independent variables was checked for each regression model using the variance inflation factor (VIF) with a VIF value greater than two used as the threshold (O’Brien 2007). Relationships between response variables was also examined via correlation matrix (Appendix 1, 2).

II.4. RESULTS

II.4.1 Overstory Data

II.4.1.1 *Pinus halepensis* Models

In the *P. halepensis* overstory dataset (96 stands), the average annual precipitation was 519 mm and ranged from 259 - 852 mm (Table 2). The elevation variable averaged 435 m and ranged from 70 - 823 m. The number of hard and soft bedrock stands was 53 and 43, while the number of stands with north and south facing aspects were 49 and 47 (Table 3). Stand age averaged 43 years and ranged 34 - 69 years.

Tree variables height, diameter, and MBAI averaged 14 m, 23 cm, 9.9 cm^2/yr, respectively, and ranged from 8 - 22 m, 14 - 42 cm, and 3.7 - 24.3 cm^2/yr (Table 4). Stand variables density, basal area, and NDVI averaged 326 trees/ha (tph), 11.9 m^2/ha, and 0.36, respectively, and ranged from 39- 880 tph, 2.7 - 28.1 m^2/ha, and 0.18 - 0.56 (Table 4).

Abiotic factors accounted for 52% and 24% of the variation in tree height and stem diameter, respectively, while for MBAI, the combination of abiotic factors and stand density, accounted for 53% of the variation (Table 5). For height and stem diameter precipitation was the most important abiotic factor, accounting for 78% and 43% of the explained variance in the models, respectively. For MBAI, density accounted for most of the explained variation (53%) in MBAI with precipitation accounting for the next largest percentage (40%). In addition, north-facing aspects significantly outperformed southern aspects and this factor accounted for 4%, 10%, and 8% of the explained variation in tree height, stem diameter, and MBAI, respectively (Figure 4A, B). A significant negative effect of elevation was found only for tree height and accounted for 5% of the explained variation. Stand density had a significant negative effect on MBAI and accounted for most of the explained variation in this variable (52%).

Table 2. Continuous explanatory variable range, averages, and standard error for the overstory dataset comprised of *Pinus halepensis* and *Pinus brutia* forest stands in Israel.

	Pinus halepensis			*Pinus brutia*		
Variable	Range	Mean	Std.Err.	Range	Mean	Std.Err.
Precipitation (mm)	259 - 842	520	15	432 - 789	602	8
Elevation (m)	70 - 823	435	20	44 - 768	371	26

Table 3. Numbers of stands with the nominal explanatory variables for the overstory dataset comprised of *Pinus halpepensis* and *Pinus brutia* forest stands in Israel.

Pinus halepensis			*Pinus brutia*		
	Aspect			Aspect	
Bedrock	North	South	Bedrock	North	South
Soft	23	20	Soft	18	17
Hard	26	27	Hard	21	18

Table 4. Dependent variables ranges, means, and standard error for the overstory data set comprised of *Pinus halepensis* and *Pinus brutia* forests in Israel.

	Pinus halepensis			*Pinus brutia*		
Variable	Range	Average	Std.Err.	Range	Average	Std.Err.
Height (m)	8 to 22	14	0.29	8 to 21	14	0.33
Diameter (cm)	14 - 42	23	0.48	15 - 32	22	0.51
MBAI$_{\text{Tree}}$ (cm^2/yr)	3.7 - 24.3	9.9	0.38	4.0 - 20.1	9	0.38
Density (tph)	39 - 880	326	17.4	85 - 1286	451	25.1
BA(m^2/ha)	2.7 - 28.1	11.9	0.49	3.6 - 35.1	16	0.69
NDVI	0.18 - 0.56	0.36	0.01	0.25 - 0.59	0.44	0.01

Table 5. Results of stepwise regression analysis of the effect of abiotic factors (explanatory) on tree and stand level forest response variables in Israel's mature (≥ 30 years) *Pinus halepensis* forests.

Response	Explanatory	R^2	DF	EV[1]	SS	F Ratio	Prob > F
Height$_{\text{Tree}}$	Precipitation	0.52	91	0.78	330.05	82.8961	**<.0001(+)**
	Aspect			0.04	17.93	4.5043	**0.0365(S<N)**
	Elevation			0.05	21.75	5.4624	**0.0216(-)**
	Age			0.13	55.57	13.9569	**0.0003(-)**
Diameter$_{\text{Tree}}$	Precipitation	0.34	90	0.43	257.17	22.4410	**<.0001(+)**
	Aspect			0.10	57.38	5.0073	**0.0277(S<N)**
	Age			0.47	278.16	24.2731	**<.0001(-)**
MBAI$_{\text{Tree}}$	Precipitation	0.53	90	0.40	221.17	46.4405	**<.0001(+)**
	Aspect			0.08	43.23	9.0763	**0.0034(S<N)**
	Density			0.52	284.39	59.7157	**<.0001(-)**
Density$_{\text{Stand}}$	Age	0.12	91	1.00	2479.94	13.1687	**0.0005(-)**
BA$_{\text{Stand}}$	Precipitation	0.24	90	0.50	2.23	14.9339	**0.0002(+)**
	Aspect			0.28	1.25	8.3637	**0.0048(S<N)**
	Elevation			0.21	0.94	6.2920	**0.0139(-)**
NDVI$_{\text{Stand}}$	Precipitation	0.39	93	0.92	0.28	54.7722	**<.0001(+)**
	Aspect			0.08	0.03	4.9559	**0.0284(S<N)**

[1] EV = Explained variation

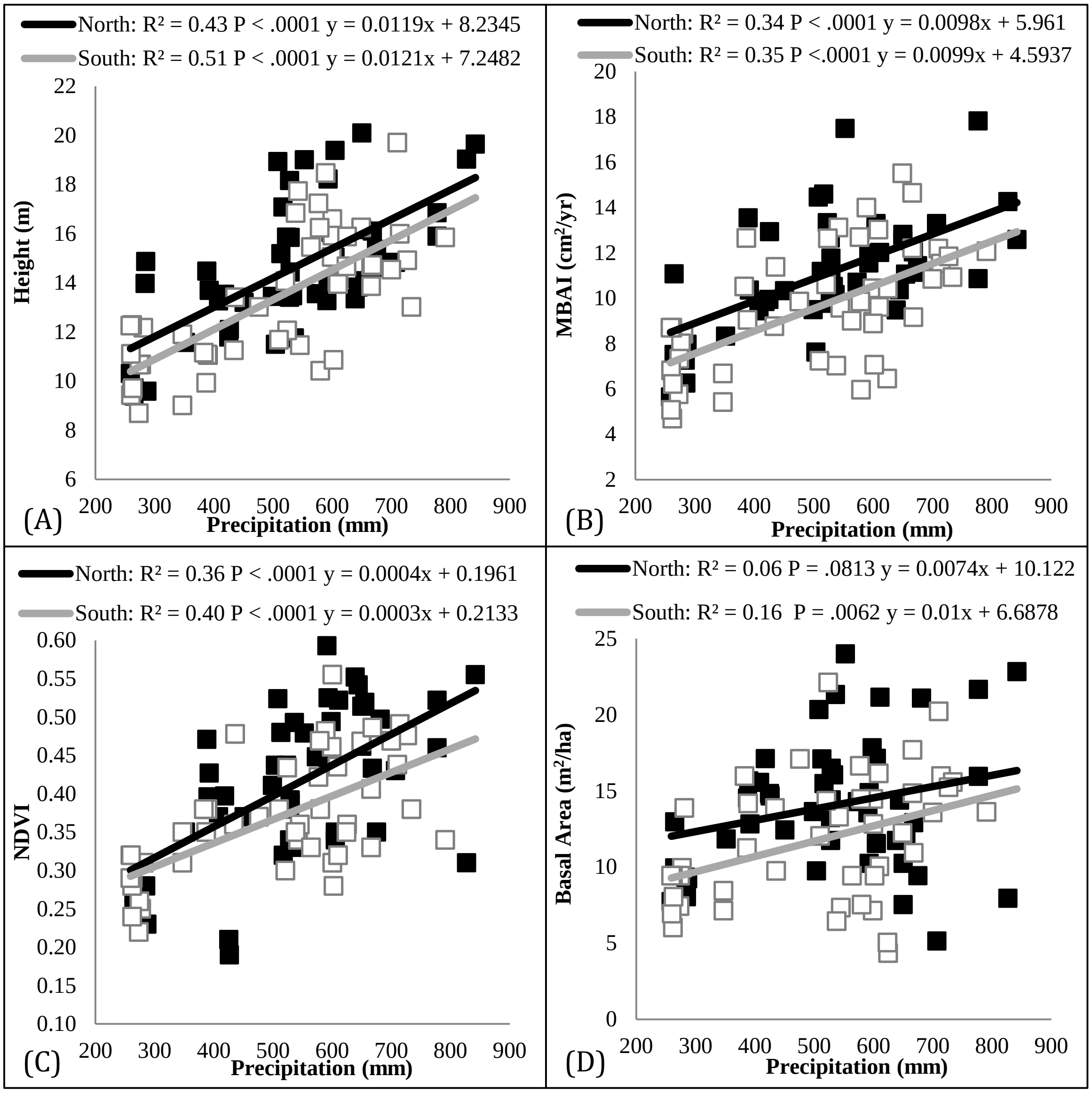

Figure 4. Relationships between precipitation and individual tree variables - height (A) and MBAI (B), and stand level variables - NDVI (C) and basal area (D) on north and south facing aspects in mature *Pinus halepensis* forests in Israel.

For stand level variables - stem basal area, and NDVI, abiotic factors accounted for 24 - 39% of the variation, respectively (Table 5). Abiotic factors failed to explain any of the variation in stand density. Similar to the tree level parameters, a positive effect of precipitation and higher performance on north vs. south facing aspects was found for stand attributes, with precipitation accounting for 50% and 92% and aspect for 28% and 8% of the explained variation in basal area and NDVI, respectively (Figure 4C, D).

No bedrock effect was found in any of the tree or stand-level variables and no effect of elevation was found for the stand level variables. Additionally, no interactions between abiotic factors were found.

II.4.1.2 *Pinus brutia* Models

In the *P. brutia* overstory dataset (74 stands), annual precipitation was 602 mm and ranged from 432 - 789 mm (Table 2). The elevation variable averaged 371 m and ranged from 44 - 768 m. The number of hard and soft bedrock stands was 39 and 35, while the number of stands with north and south facing aspects were 39 and 35 (Table 3). Stand age averaged 42 years and ranged from 32 to 61.

Tree variables height, diameter, and MBAI averaged 14 m, 22 cm, 9.2 cm^2/yr, respectively, and ranged from 8 - 21 m, 15 - 32 cm, and 4.0 - 20.1 cm^2/yr (Table 4). Stand variables density, basal area, and NDVI averaged 451 tph, 15.7 m^2/ha, and 0.44, respectively, and ranged from 85 - 1286 tph, 3.6 - 35.1 m^2/ha, and 0.25 - 0.59 (Table 4).

Abiotic factors generally explained less variance in stand and tree characteristics for *P. brutia* than for *P. halepensis*, and overall, there was less consistency in the way by which abiotic factors influenced the different response variables. Abiotic factors accounted for 43% and 28% of the variation in tree height and stem diameter in *P. brutia*, while for MBAI, the combination of abiotic factors and tree density, accounted for 43% of the variance (Table 6). A significant aspect × elevation interaction occurred for tree height, stem diameter, and MBAI and accounted for 31%, 17%, and 26% of the explained variance (Table 6). Tree height significantly decreased with increasing elevation on north facing aspects and tended to increase with elevation on southern aspects, however this increase was not significant (Figure 5A). Similar trends were found for stem diameter and MBAI as performance for both variables was not significantly related to elevation on south facing aspects but significantly decreased on north facing aspects with increasing elevation (Figure 5C, D). From another perspective, tree level parameters were higher on south than on north facing aspects at high elevations while this was reversed at low elevations. (Figure 5A, C, D).

Table 6. Results of stepwise regression analysis of abiotic factors (explanatory) affecting tree and stand level forest (response) variables in Israel's mature (≥ 32 years) *Pinus brutia* forests.

Response	Explanatory	R^2	DF	EV^1	SS	F Ratio	Prob > F
Height$_{\text{Tree}}$	Precipitation	0.43	66	0.09	20.02	4.4612	**0.0385(+)**
	Bedrock			0.14	31.50	7.0200	**0.0101(H<S)**
	Aspect			0.10	21.86	4.8723	**0.0308(S<N)**
	Precipitation*Aspect			0.08	17.49	3.8993	**0.0525**
	Elevation				9.67	2.1560	0.1468
	Aspect*Elevation			0.31	68.02	15.1616	**0.0002**
	Age			0.23	49.92	11.1265	**0.0014(+)**
Diameter$_{\text{Tree}}$	Precipitation	0.28	68	0.11	53.23	3.8471	**0.0539(+)**
	Aspect				3.71	0.2679	0.6064
	Elevation				25.04	1.8099	0.1830
	Aspect*Elevation			0.17	80.82	5.8412	**0.0183**
	Age			0.66	315.13	22.7745	**<.0001(+)**
MBAI$_{\text{Tree}}$	Aspect	0.43	67		12.63	2.4381	0.1231
	Elevation				8.66	1.6726	0.2004
	Aspect*Elevation			0.26	87.70	16.9288	**0.0001**
	Density			0.68	232.35	44.8503	**<.0001(-)**
Density$_{\text{Stand}}$	Bedrock	0.16	69	0.17	1325.07	4.2065	**0.0441(H<S)**
	Elevation			0.43	3315.88	10.5264	**0.0018(+)**
	Age			0.40	3067.16	9.7368	**0.0026(-)**
BA$_{\text{Stand}}$	Precipitation	0.29	65		0.07	0.3475	0.5576
	Bedrock			0.18	1.02	4.7656	**0.0327(H<S)**
	Precipitation*Bedrock			0.25	1.44	6.7125	**0.0118**
	Aspect				0.30	1.4179	0.2381
	Bedrock*Aspect			0.22	1.25	5.8177	**0.0187**
	Elevation				0.77	3.5777	0.0630
	Aspect*Elevation			0.16	0.89	4.1623	**0.0454**
NDVI$_{\text{Stand}}$	Precipitation	0.30	68	0.32	0.05	14.6622	**0.0003(+)**
	Bedrock				0.01	2.9954	0.0880
	Precipitation*Bedrock			0.19	0.03	8.6880	**0.0044**

Table 6 continued

Response	Explanatory	R^2	DF	EV^1	SS	F Ratio	Prob > F
	Aspect			0.14	0.02	6.2136	**0.0151(S<N)**
	Elevation			0.28	0.04	12.7232	**0.0007(+)**

[1] EV = Explained variation

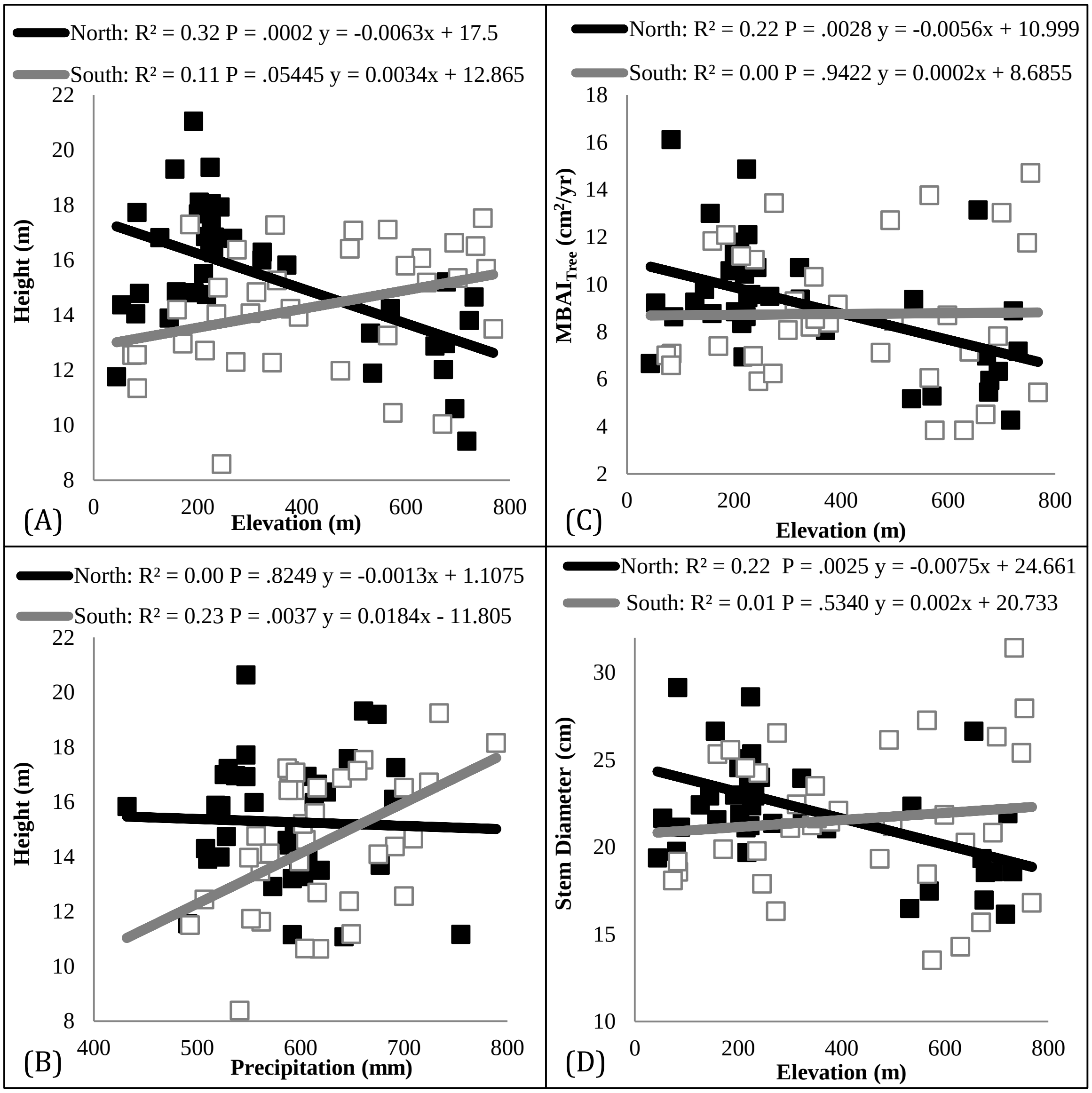

Figure 5. Relationships between tree variables - height (A & B), MBAI (C), and stem diameter (D) reflecting a significant interaction between aspect and elevation (height, MBAI, stem diameter) or precipitation (height) in mature *Pinus brutia* forests in Israel.

Precipitation as a main effect was found to be significant for *P. brutia* tree height, accounting for 9% of the variation. Likewise a precipitation × aspect interaction was also found to be significant and accounted for 8% of the variation (Figure 5B). Tree height increased with precipitation on south facing aspects but was uninfluenced by a change in precipitation on northern aspects. Finally, tree height was found to be significantly higher on soft bedrock vs.

hard bedrock, a main effect that accounted for 14% of the explained variation. Average stem diameter increased with precipitation, although it did not reach the $P < 0.05$ threshold ($P = 0.0506$).

Finally, in addition to the aspect × elevation interaction, MBAI was negatively influenced by density, which accounted for 68% of the explained variation (Figure 5C).

For stand level variables - tree density, basal area, and NDVI, abiotic factors accounted for 16% - 30% of the variation in *P. brutia* forests (Table 6). Abiotic factors explained the most variance ($R^2 = 30\%$) for NDVI and the least for stand density ($R^2 = 16\%$). Aspect × elevation interaction was significant for basal area only, and accounted for 22% of the variation (Figure 6B). Based on this interaction, basal area significantly increased with increasing elevation on south facing aspects but was not related to elevation on northern aspects.

Stand basal area for *P. brutia* was significantly influenced by two additional interactions - precipitation × bedrock and aspect × bedrock (Figure 6A, C), accounting for 25% and 22% of the explained variation, respectively (Table 6). Basal area increased significantly with precipitation on soft bedrock but was unchanged on hard bedrock. Comparing hard vs. soft bedrock on north facing aspects did however result in a significant effect with higher basal area being found on soft bedrock types (Figure 6C).

Only 16% of the variation in stand density was explained by bedrock, elevation, and age, which explained 17%, 43%, and 40% of the variation, respectively (Table 6). Overall, stand density was significantly higher on soft vs. hard bedrock and was positively influenced by increasing elevation. NDVI was influenced by two main effects - aspect and elevation, and one interaction - precipitation × bedrock, accounting for 14%, 28%, and 19% of the explained variation, respectively, within NDVI was found to be significantly higher on north vs. south facing aspects (Figure 6D). NDVI was also found to increase positively with increasing elevation on hard bedrock but showed no effect on soft bedrock.

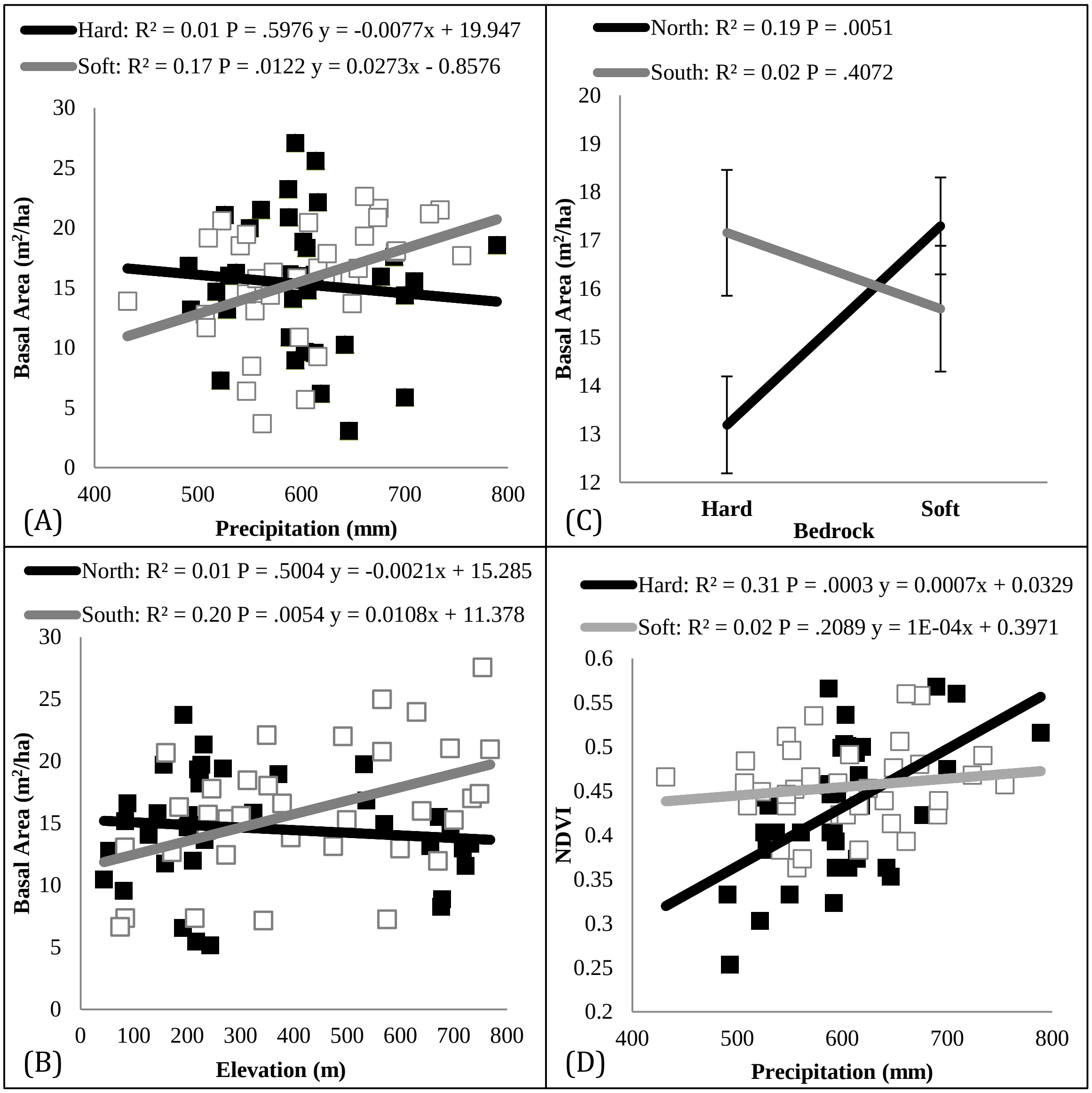

Figure 6. Relationships between stand variables - basal area (A, B, C) and NDVI (D), and interacting abiotic factors (bedrock, precipitation, elevation, aspect) for mature *Pinus brutia* forests in Israel.

Overall, *P. brutia* performance appeared to positively correspond to increases in water availability, e.g. higher precipitation and elevation, North vs. South facing aspect, and soft vs. hard bedrock, however these effects were not consistent throughout the studied range of forest variables.

II.4.1.3 Combined Species Models

The total number of stands in the combined dataset was 145 with 71 *P. halepensis* and 74 *P. brutia* stands. The reduced number of *P. halpensis* stands, compared to the previous analysis, was due to the exclusion of stands below 400 mm AAP. In the combined analysis *P. halepensis* AAP was 594 mm with a range from 408 - 842 mm, average elevation was 431 m with a range from 70 - 823 m, number of stands on hard and soft bedrock was 40 and 31, and north and south facing aspects was 39 and 32. The distribution of *P. brutia* stands was the same as previously described. Average stand age was 42 years and ranged from 32 to 69.

For *P. halepensis,* the average tree variables height, diameter, and MBAI averaged 15 m, 23 cm, 10.4 cm^2/yr, respectively, with a range from 10 - 22 m, 14 - 35 cm, and 3.7 - 23.4 cm^2/yr. Stand variables density, basal area, and NDVI averaged 345 tph, 12.9 m^2/ha, and 0.39, respectively, with a range from 39 - 880 tph, 2.7 - 28.1 m^2/ha, and 0.18 - 0.56. For *P. brutia,* tree and stand level variables were the same as previously described.

Significant differences between *P. halepensis* and *P. brutia* were found in five forest variables (Appendix 3, Figure 7). Stem diameter and MBAI were significantly higher for *P. halepensis* than *P. brutia,* while no difference was seen for tree height. A species × bedrock interaction was found for tree height. Height was significantly higher on hard bedrock for *P. halepensis* vs. *P. brutia* but no differences were seen on soft bedrock. At the stand level, density, basal area, and NDVI were significantly higher for *P. brutia* than *P. halepensis.* In addition, a species × bedrock interaction was found for basal area where increasing age caused a increasing effect on *P. brutia* but a decreasing effect for *P. halepensis,* however neither trend was significant.

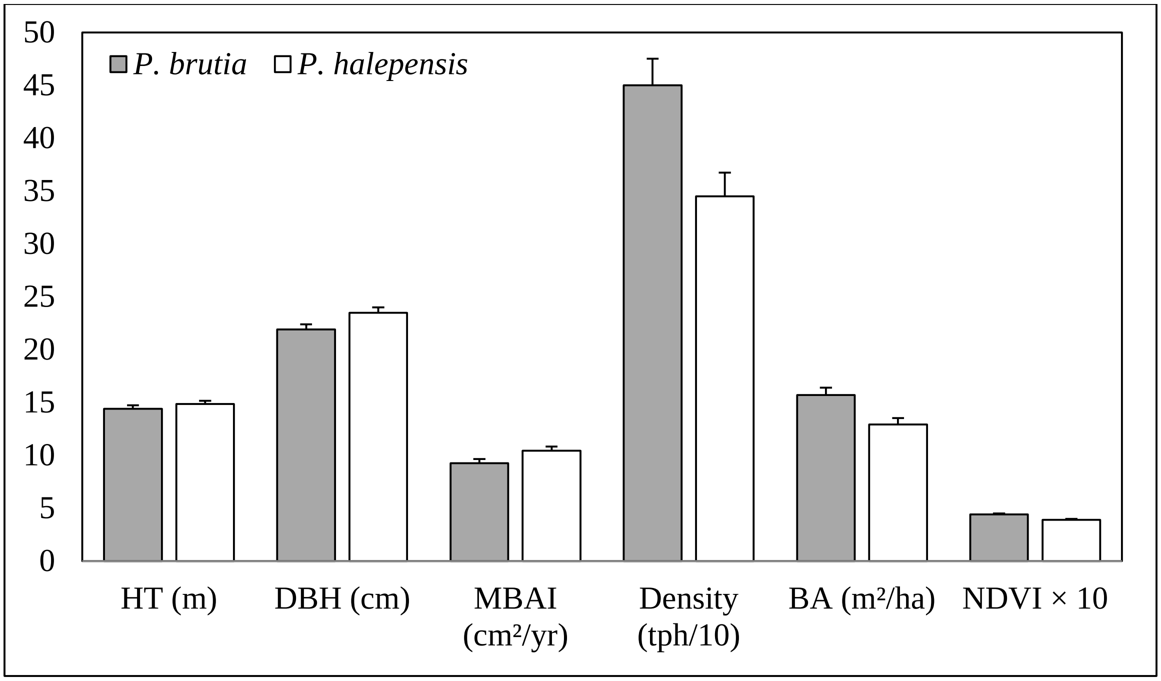

Figure 7. Average tree (HT, DBH, MBAI) and stand (density, BA, NDVI) level variables for combined overstory dataset composed of *Pinus halepensis* and *Pinus brutia* forest stands in Israel. Error bars represent standard error of the mean.

II.4.2 Understory Data

II.4.2.1 *Pinus halepensis* Models

In the understory study, annual precipitation for *P. halepensis* stands averaged 503 mm and ranged from 259 - 777 mm (Table 7). Elevation was 381 m on average with a range of 83 - 708 m. The number of hard and soft bedrock stands was 23 and 25, while the number of stands on both north and south facing aspects were 24 (Table 8). Overstory basal area had a mean of 9.9 m^2/ha with a range of 2.8 - 19.4 m^2/ha (Table 7). Stand age averaged 53 years and ranged 44 to 88.

Understory biovolume variables total, oak, and pine, averaged 0.169, 0.029, and 0.007 m^3/m^2, respectively, with a range from 0 - 1.77, 0 - 0.58, and 0 - 0.25 m^3/m^2, respectively (Table 9).

Abiotic factors accounted for 24%, 48% and 33% of the variation in understory pine (regenerating pines), oak (regenerating oaks), and total woody (trees, shrubs and vines) volumes. For understory pine volume, bedrock accounted for 78% of the explained variation within the model (Table 10). Hard bedrock supported significantly less pine volume than soft. The remaining 22% of explained variation within the pine volume model was accounted for by precipitation, although it did not reach the $P < 0.05$ threshold ($P = 0.0594$). For understory oak volume, precipitation accounted for 45% and overstory BA for 32% of the explained variation (Table 10). Understory Oak volume increased with precipitation but decreased with overstory basal area. In addition, a bedrock × elevation was also found to be significant, however it was difficult to interpret this relationship as only 13 stands (7 hard bedrock stands, 6 soft bedrock stands) had any recordable oak volume and were poorly distributed along the elevation gradient. Variation in total understory volume was best described by precipitation and elevation (Table 10) accounting for 81% and 19% of the explained variation, respectively. Precipitation had a positive effect (Figure 8) and elevation had a negative effect on total understory woody volume.

Table 7. Continuous explanatory variable range, averages, and standard error for the understory dataset of *Pinus halepensis* and *Pinus brutia* forest stands examined in Israel.

	Pinus halepensis			*Pinus brutia*		
Variable	Range	Mean	Std.Err.	Range	Mean	Std.Err.
Precipitation (mm)	259 - 777	504	21	432 - 714	588	11
Elevation (m)	83 - 708	381	28	58 - 734	300	35
Basal Area (m^2/ha)	2.8 - 19.4	9.9	0.6	2.4 - 21.5	12.4	0.7

Table 8. Numbers of stands with the nominal explanatory variables for the undestory dataset comprised of *Pinus halpepensis* and *Pinus brutia* forest stands in Israel.

Pinus halepensis			*Pinus brutia*		
	Aspect			Aspect	
Bedrock	North	South	Bedrock	North	South
Soft	12	13	Soft	8	8
Hard	12	11	Hard	7	9

Table 9. Response variable range, average and standard error for the understory dataset of *Pinus halepensis* and *Pinus brutia* forest stands examined in Israel.

	Pinus halepensis			*Pinus brutia*		
Variable	Range	Mean	Std.Err.	Range	Mean	Std.Err.
Total (m^3/m^2)	0 - 1.77	0.169	0.046	0 - 1.80	0.237	0.079
Oak (m^3/m^2)	0 - 0.58	0.029	0.016	0 - 1.35	0.117	0.051
Pine (m^3/m^2)	0 - 0.25	0.007	0.007	0 - 0.02	0.001	0.001

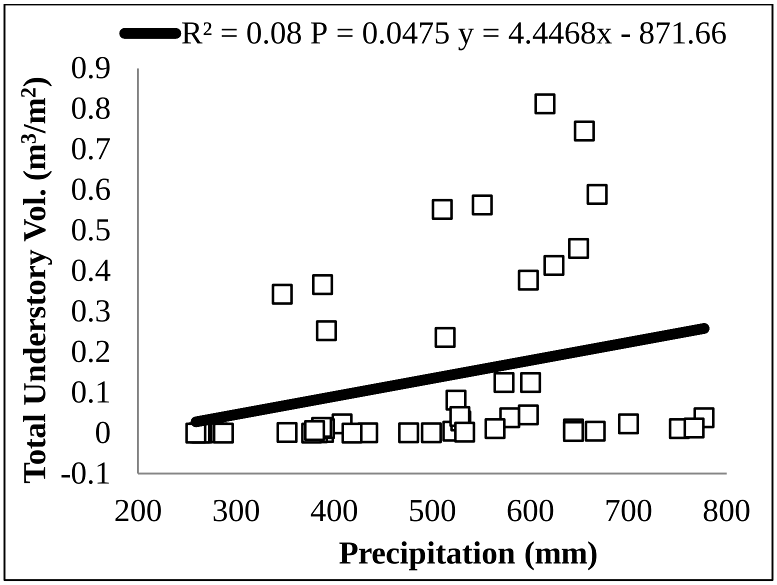

Figure 8. Relationship between total understory woody volume and precipitation for *Pinus halepensis* forests in Israel.

II.4.2.2 *Pinus brutia* Models

In the understory plot set up (32 plots), annual precipitation for *P. brutia* stands averaged 588mm and ranged from 432 - 714 mm (Table 7). Average elevation was 300 m with a range of 58 - 734 m. The number of stands on both hard and soft bedrock was 16, while the number of stands with north and south facing aspects was 15 and 17, respectively (Table 8). Overstory basal area had a mean of 12.4 m^2/ha with a range of 2.4 - 21.5 m^2/ha (Table 7). Stand age averaged 53 years and ranged 45 to 64.

Table 10. Results from stepwise regression analysis of the effect of abiotic factors on understory volume in *Pinus halepensis* and *Pinus brutia* forests.

Tree	**Response**	**Explanatory**	**R^2**	**DF**	**EV[1]**	**SS**	**F Ratio**	**Prob > F**
P. halepensis	Pine	Precipitation	0.24	45		1009.03	3.7423	0.0594
		Bedrock			0.78	3587.93	13.3068	**0.0007(H<S)**
	Oak	Precipitation	0.48	41	0.45	3832.45	25.4478	**<.0001(+)**
		Bedrock				152.97	1.0157	0.3194
		Elevation				73.79	0.4900	0.4879
		Bedrock*Elevation			0.11	985.01	6.5406	**0.0143**
		Basal Area			0.32	2723.52	18.0844	**0.0001(-)**
		Age			0.10	826.23	5.4862	**0.0241(+)**
	Total	Precipitation	0.33	45	0.81	7860.82	21.3543	**<.0001(+)**
		Elevation			0.19	1803.72	4.8999	**0.0320(-)**
P. brutia	Pine	No model produced						
	Oak	Precipitation	0.13	29		1527.19	3.8963	0.0580
		Aspect				1282.92	3.2731	0.0808
	Total	Precipitation	0.12	31		2073.00	4.3108	**0.0465(+)**

[1] EV = Explained Variation

Understory woody volume variables total, oak, and pine averaged 0.237, 0.117, and 0.001 m^3/m^2, respectively, with a range from 0 - 1.80, 0 - 1.35, and 0 - 0.02 m^3/m^2 (Table 9).

Understory vegetation development in *P. brutia* forests appeared to be less influenced by abiotic factors than in *P. halepensis* forests and insensitive to overstory canopy coverage or basal area. Abiotic factors accounted for 13% and 12% of the variation in understory oak and total woody volumes, but had no discernible effect on pine regeneration (Table 10). Precipitation and aspect accounted for 13% of the variation in oak volume but neither factor was significant, although precipitation corresponded to a positive effect ($P = 0.058$).

Similarly, for total understory woody volume in *P. brutia* stands, precipitation accounted for 12% of the variation and had a significant positive effect with increasing precipitation (Table 10).

II.4.2.3 Combined Species Model

The total number of stands in the combined dataset was 64 with *P. halepensis* and *P. brutia* both having thirty-two stands. The reduced number of *P. halepensis* stands, from forty-eight to thirty-two was for the same reason as mentioned in the overstory combined dataset section. In this set up, AAP for *P. halepensis* stands was 586 mm with a range from 408 - 777 mm, average elevation was 384 m with a range from 83 - 697 m, number of stands on both hard and soft bedrock was 16, as well as 16 stands on both north and south facing aspects. Stand age averaged 53 years and ranged 44 to 88.

Overstory basal area had a mean of 11.1 m^2/ha with a range of 4.0 - 19.4 m^2/ha. Distribution for *P. brutia* stands was the same as previously described.

A significant difference in understory development between *P. halepensis* and *P brutia* stands was only found for understory pine volume (Appendix 4, Figure 9). A significant species × bedrock interaction on pine regeneration was found indicating that on soft bedrock pine regeneration was much higher in *P. halepensis* than in *P. brutia* stands while on hard

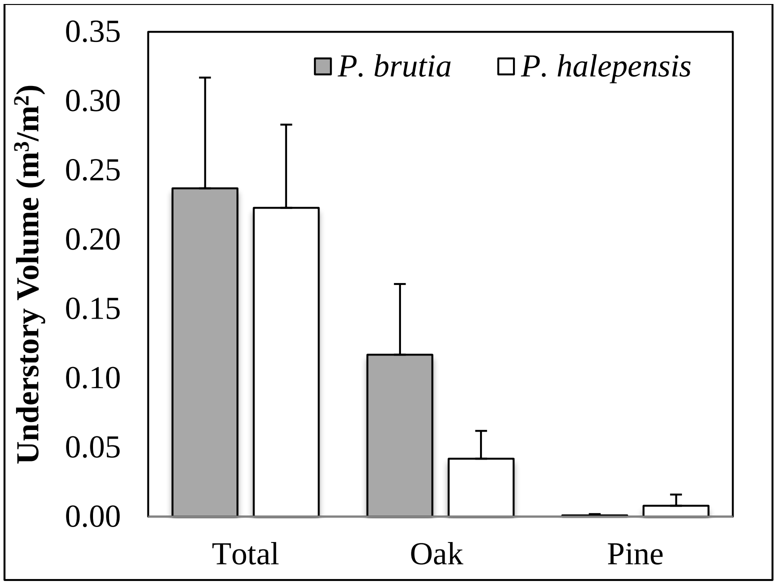

Figure 9. Average understory volume for *Pinus halepensis* and *Pinus brutia* forest stands in Israel. Error bars represent standard error of the mean.

bedrock it was similar among the two species. Notably for *P. brutia*, only five stands had pine in the understory.

II.5. DISCUSSION

II.5.1 Overview

Water-availability is generally accepted as limiting the performance and growth of Mediterranean pine forests (Pigott and Pigott 1993). Water stress occurs during the hot, dry summer season where little to no precipitation occurs. Stress caused by a lack of precipitation both moderated by landscape features (aspect, slope and parent material). Cooler temperatures with elevation can also relieve moisture stress, but notable seasonal variation in temperature can also negatively affect plant performance in Mediterranean regions (Krammer et al. 2000; Sabaté et al. 2002; Vincente-Serrano et al. 2010). In addition, the role of understory development is becoming increasingly important as Israel's mature forest near the end of their life expectancy (Osem et al. 2008). Understanding whether these forests can transition from an artificially planted to naturally regenerative system has been under investigation recently (Osem et al. 2009, 2011) as well as how management can further this process (Calev et al. 2016), increase biodiversity (Torras and Saura 2008; Ginsberg 2006;Maestre and Cortina 2004; Gómez-Aparicio et al 2009), and manipulate the overstory-understory relationship (Cooper et al. 2014; Coll et al. 2010).

I examined how precipitation, and other abiotic factors known to affect water availability, influenced the growth and performance of mature trees and understory development in Israel’s mature *P. halepensis* and *P. brutia* forests. For *P. halepensis*, consistent positive correlations between tree and stand performance metrics and precipitation in addition to higher performance on north vs. south facing aspects supported the common view of these forests being limited by water availability. In contrast, for *P. brutia* forests abiotic influences were generally less clear due to overall complex and inconsistent interactions, which suggest the involvement of some other factors not previously accounted for. Overall, these results support some of my hypotheses while rejecting some others.

II.5.2 *Pinus halepensis* Overstory and Understory Response to Abiotic Factors

P. halepensis forests responded to precipitation for both overstory tree and stand level parameters, with the positive linear relationship found suggesting that precipitation was uniformly limiting throughout the entire precipitation gradient. This result is surprising in light of previous studies suggesting that precipitation is limiting to a certain extent, above which factors such as soil depth, bedrock type, and nutritional content of the soil becomes more important (Schiller 2000; Rabinowitch 1985) or that a waning effect exists (Kadmon and Danin 1999). To my knowledge, this is the first study in Israel that incorporates the full extent of this precipitation limitation. In regards to woody understory development (volume), I found a significant positive relationship with precipitation along the entire precipitation gradient, further supporting similar studies in *P. halepensis* forests in Israel (Osem 2009; 2011).

Water availability may have also been moderated by aspect, as better performance was consistently found on north vs. south facing forests in *P. halapensis* stands. The effect of aspect likely reflected differences in solar radiation load and temperature (Pigott and Pigott

1993); where evaporative demand was lowered on north-facing slopes. Similar results have been found elsewhere in the Mediterranean region (Al Omary 2011; Sternberg and Shoshany 2001) and in other ecosystems (Stage and Salas 2007; Coble et al. 2001; Fekedulegn et al. 2003). The moderating effect of aspect seemed to be confined to the overstory as the understory volume in these forests was unaffected by this factor. This however contradicts the understory results found by Osem et al. (2009, 2011) where performance was significantly better on North vs. South facing stands.

Although my findings regarding precipitation and topographic aspect generally supported my hypothesis, some of my findings deviate from previous work in two important ways. First, previous studies in Israel have highlighted the significant influence of hard vs. soft calcareous bedrock, concluding that bedrock type was a major factor in determining forest performance (Heth 1965; Schiller 1972, 1982; Seligman and Douer 1971; Rabinowitch 1985). However, my results found no effect of bedrock for any of the overstory characteristics considered. I may have found no bedrock effect in mature forests because, relative to earlier studies, I incorporated a wider spatial distribution of forest stands. Changes in spatial scale can often result in an altered view of ecological processes (Wiens 1989), which does not support a full rejection of a potential modifier of tree function but rather suggests it is important at a resolution not captured by a given study. As opposed to the overstory indices, understory *P. halapensis* sapling volume was positively affected by bedrock type, supporting my hypothesis of soft-bedrock having better water holding capacity thus positively influencing tree performance. This may suggest that earlier studies, which were often done in younger trees and within narrower distributions of climate, captured a juvenile effect that did not persist in more mature trees.

Second, in previous work, the importance of aspect has been shown to have a waning effect with increasing precipitation for overstory forest performance (Dorman et al. 2013b; Schiller 1972; Olarieta et al., 2000). Once again I did not find support for this hypothesis. The deviation of my results from these past studies may reflect differences in the scale of the investigations, in the age of the trees, in the phase of stand dynamics (extent of self-thinning) and/or management (history of thinning treatments) at the time of measurement.

Elevation had a negative influence on *P. halepensis* tree height and basal area as well as on woody understory development. This result did not support my hypothesis, as I expected a positive relationship with increasing elevation, corresponding to lower temperatures and reduced water loss due to evapotranspiration. The negative effect on tree height supports an earlier study in Israel by Bolotin (1969) who also found a negative relationship between elevation and tree growth in *P. halepensis* stands. The negative effect on basal area may correspond to a positive increase in density, although this relationship was not significant based on the stepwise model. Still, according to a one-way analysis of density and elevation there was an increase in density as elevation increased. No further relationships were drawn based on this effect. The negative effect of elevation on tree growth may be attributed to a co-occurring decrease in winter temperature and soil depth. In the forested region of Israel average annual temperatures in the winter is between 12°C and 15°C and summer is 20°C and 25°C (Dorman et al. 2015). It is suggested that during the winter to early spring, when soil water availability is high, temperature may limit growth. In addition, decreasing soil depth resulting from soil erosion on high mountain slopes might also play an important role (Bolotin 1969; Tomaselli 1977). Similar studies outside of Israel have also found a negative relationship between elevation and tree performance (Trasobares et al. 2004; Broncano and Retana 2004; Al Omary 2011). In regards to understory development, the negative relationship found with elevation may also be explained in the same way. However, this effect may not correspond in the same manner throughout the Mediterranean region (Coll et al. 2010). Additional research is needed to further our understanding regarding elevation and temperature effects on forest performance in water limited Mediterranean forests.

Greater tree density decreased individual tree growth the studied *P. halepensis* stands, a common response in forests undergoing inter-tree competition for resources (Oliver and Larson 1996; Zeide 2002) or growing space (Zeide et al. 1991). Once the density effect was accounted for the influence of precipitation on tree performance was still evident. Density itself, however, was not influenced by abiotic factors. This lack of density response could have been the result of some combination of management (thinning or planting density), drought, and insect outbreaks. Indeed, the pine bast scale (*Matsucoccus josephi*) has caused widespread mortality in many of these *P. halepensis* stands with dense stands being more susceptible to these outbreaks (Mendel 1987, 2000).

Looking at overstory-understory interactions in *P. halepensis* stands, I found that overstory canopy coverage did not have an effect on total understory cover but did negatively influence understory oak volume. Recent studies in the Mediterranean region have highlighted that in dense stands of *P. halepensis* and *P. brutia,* overstory coverage has had a greater effect on understory development than topographic and climatic variables (Mitsopoulos and Xanthopoulos 2016). However, in lower density areas, overstory coverage has had a minimal impact on understory development relative to climatic factors (Coll et al. 2010). This also appears to be the case in Israel's mature *P. halepensis* forests. Two important factors not considered in this investigation for understory development are grazing and human disturbances. Moderate to heavy grazing regimes have been ongoing since the inception of these forests and are used as an effective tool for reducing the fuel load (Osem et al. 2008; Carmel and Kadmon 1999; Kaplan 2011). Similarly, thinning regimes have been prescribed on decadal intervals and regular recreational usage and wildfire mitigation in these forests have probably had mixed effects on understory development (Bonneh 2000; Perevolotsky and Sheffer 2009; Kaplan 2011).

II.5.3 *Pinus brutia* Overstory Response to Abiotic Factors

The relationships between abiotic factors and *P. brutia* forest provided only partial support for my hypotheses. Simply stated, my results for the overstory *P. brutia* dataset are puzzling and I was unable to provide a complete explanation for the found abiotic interactions, as these were inconsistent in their effect on tree and stand level parameters. For example, an aspect × elevation interaction showed individual tree performance to decrease on northern aspects with increasing elevation, but no change in tree performance with increasing elevation was found on southern aspects. An opposite pattern however, was seen with stand basal area which increased on southern aspects with increasing elevation, but did not change with elevation on northern aspects. Similarly, a precipitation × bedrock interaction had opposing effects on stand level characteristics - basal area and NDVI, where basal area increased significantly with precipitation on soft but not hard bedrock, while the exact opposite was found for NDVI which increased with precipitation significantly on hard but not on soft bedrock. No conclusive explanation was found that would account for these discrepancies. It appears that other factors not accounted for, possibly management and or other disturbances, might have had an important effect on the performance of *P. brutia* overstory. In the following I propose two explanations that may partially account for these results.

The aspect × elevation interaction had a significant effect for individual tree characteristics (height, diameter, and MBAI) and stand basal area. Based on the individual tree parameters, it appears that *P. brutia* sensitivity to temperature may account for the negative effect of elevation found on north facing aspects as north facing aspects are somewhat cooler than southern aspects due to lower solar radiation load (Pigott and Pigott 1993). The native distribution of *P. brutia* reflects this sensitivity as *P. brutia* grows well between elevations of 300 - 600 m a.s.l. on northern aspects and between elevations of 1200 - 1400 m a.s.l. on southern aspects, respectively, corresponding to the differences in temperature on north vs. south facing aspects (Quezel 1979, 2000; Nahal 1986). This explanation might explain the negative effect of elevation on north facing aspect but does not adequately explain why stands growing on south facing aspects showed no response to elevation, nor does this explain the opposing effect with stand basal area. An alternative explanation could be that stand density, which was found positively related with elevation, was the reason for the decreased individual tree performance on high elevation sites. However, I could not find an explanation for why this effect was only found on southern aspect and not on northern ones.

The precipitation × bedrock interaction on *P. brutia* stand basal area was also difficult to interpret. Assuming water-availability is the limiting factor, it was expected that an increase in precipitation would increase stand performance more so on hard vs. soft bedrock, as soft bedrock is assumed to have higher water holding capacity than hard one. This did in fact occur with NDVI, where performance increased significantly with precipitation on hard bedrock while stands on soft bedrock were not influenced by precipitation. It appears that stands on soft bedrock were less limited by water-availability than those growing on hard bedrock. Similarly, tree height increased significantly with increasing precipitation on south but not on north facing aspect. Here again, it appears that stands on north facing aspects were less limited by water-availability than those growing on south facing aspects. Within this context, it is important to note that *P. brutia* stands were planted in a narrower range of rainfall levels (432 - 789 mm yr^{-1}) compared to *P. halepensis* stands (259 - 842 mm yr^{-1}) making precipitation level generally less effective for *P. brutia*.

The bedrock × aspect interaction on *P. brutia* basal area was also difficult to interpret. On north facing aspects stands growing on soft bedrock had significantly higher basal area than stands on hard bedrock, corresponding to water-availability being higher on soft vs. hard bedrock sites. Surprisingly, basal area was not significantly affected by bedrock type on south facing slopes. Here again, it is hypothesized that variation in management effects on stand density (e.g. thinning) might have had an important role in controlling basal area.

In Israel, *P. brutia* stands have not experienced major tree mortality like has been reported with *P. halepensis* due to droughts (Schiller 2000, 2009; Ungar et al. 2013) and insect outbreaks (Mendel 1987; 2000). Nor has there been evidence of major tree mortality due to inner tree competition as these stands are below the self-thinning line for *P. brutia* according to growth and yield models for Syria (Shater et al. 2011) and Lebanon (De Miguel et al. 2010). In my study, abiotic factors weakly explained (<11%) of the variation in stand density and it is therefore hypothesized that variation in management and/or other disturbances unaccounted for, might be controlling the existing variation in forest performance. This might explain some of the inconsistencies based on previously discussed interactions and it is further hypothesized that this might explain the relationship between density and elevation. Density was found to have a significant negative effect on tree growth, explaining 68% of the variation for MBAI, as well as on tree height (Appendix 2). It is possible that since high elevation stands are less accessible, these were less intensively treated with thinning because they were recognized early on as unprofitable forests. Further research is needed to better understand the variation in the performance of *P. brutia* stands in Israel.

In addition to the precipitation × bedrock interaction, bedrock was found to have a sole effect on *P. brutia* tree height, stand density, and basal area. As expected, performance on soft bedrock was higher than hard one and explained 14%, 17%, and 18% of the variation in tree height, density, and basal area the second explained variance for height and density models. Tree height responded as expected to bedrock, performing better on soft vs. hard bedrock sites presumably because of increased water availability. Surprisingly, no studies were found on the direct significance of bedrock type in *P. brutia* forests. *P. brutia* has been known, however, to grow on different bedrock types (e.g., limestone, marly limestone, conglomerate) but it has generally favored fissured soils on marly limestones (Boydak 2006; Quezel 2000). *P. brutia* was shown to grow poorly on serpentine, gnays and volcanic rocks because of poor nutrient availability (Boydak 2006), nor has it tolerated poorly drained soils (Quezel 2000).

II.5.4 *Pinus brutia* Understory Development Response to Abioitc Factors

Understory development in *P. brutia* stands was poorly explained by abiotic factors and was also uninfluenced by overstory canopy coverage. Abiotic factors explained less than 14% of the variation in understory development and did not explain any of the variation for regenerating pine volume, although this could be due to minimal pine volume being recorded with only five sites (out of 32) having any recordable amount of regenerating pines. The remaining 86% of unexplained variation in total woody understory development could be due to variable grazing regimes (Osem et al. 2015), variable management causing overcrowding in some of the sites, or variation in genetics (Boydak et al. 2003). At the present stand densities typical to Israel's mature *P. brutia* forests this species appears to have limited ability to regenerate under its own dense canopy.

II.5.5 Species Comparison

An important factor not considered with this study is the variations in genotypes planted in Israel for both *P. halepensis* and *P. brutia.* Provenance tests have shown significant intra-species variation for both species (Weinsein 1989a, 1989b, Schiller and Waisel 1989). In addition, provenance tests have also found *P. halepensis* out performing *P. brutia* (Bariteau

1992; Grunwald and Schiller 1988). Similar results have also been found in Italy's arid regions while in more sub-humid regions no growth differences were found (Eccher et al. 1987). During the early years of tree planting in Israel, seeds from across the Mediterranean were imported and planted but no documentation was kept regarding which seed source was planted where. Subsequently, it is unknown how many varieties of seed might be represented in this dataset. Therefore, in the interpretation of my combined species analyses it should be noted that the maladaptation of species' ecotypes to their 'new' range could be as large as the differences among species.

The combining of both species datasets under a similar abiotic combination has, to my knowledge, never been done before and has yielded two important results. First, individual tree growth was found to be significantly higher in *P. halepensis* than *P. brutia,* while at the stand level *P. brutia* stands were more dense and subsequently had higher basal area and NDVI values. This was somewhat surprising as *P. brutia* is an exotic species planted in Israel and yet, at the stand level, it appears to be doing better than the native *P. halepensis.* The contrasting response of tree height vs. hard bedrock for both species did seem to indicate that *P. brutia* was being negatively influenced because of higher stand density and subsequently lower water-availability (Dorman et al. 2015). As mentioned previously, *P. brutia* has not experienced the level of natural mortality due to drought and insect outbreak as has *P. halepensis*. It is probable that given similar stand densities, *P. brutia* may have outperformed *P. halepensis* also at the individual tree level. This could not be verified as to my knowledge no long-term provenance and species trials have been established in Israel. Differences between the native and non-native species were also found based on the understory data, as pine regeneration was significantly higher for the native, *P. halpensis,* vs. non-native, *P. brutia.*

Finally, NDVI integrates the response of all plants to environmental factors and the NDVI models for both species clearly showed a strong positive effect of precipitation. NDVI was also significantly higher on north vs. south facing aspects, another metric of water availability. Trends in the NDVI metric merely highlight that water-availability appears to be the principle limiting factor at the ecosystem level across the range of both species. Whether a species' individual tree or stand metric's of tree function respond similarly to abiotic factors as NDVI could reflect unique aspects of the species or differences in management.

CHAPTER III

CONCLUSION

I hypothesized forest growth and performance in mature pine forests in Israel would increase with indices of water-availability. My overstory dataset results mostly supported my hypotheses for *P. halepensis* forests, as changes in precipitation were found to be the main determining factor influencing forest performance with an additional positive influence of north vs. south facing aspects.

Abiotic influences on *P. brutia* forests were more complicated as interacting effects between the four abiotic factors were prevalent, mostly aspect × elevation for individual tree characteristics and precipitation × bedrock for stand level ones. Temperature limitation may have had a more important influence than previously thought, although further investigation will be needed.

Understory development was positively related to precipitation in *P. halepensis* and *P. brutia* forests, while overstory canopy coverage had minimal influence on understory development. For unknown reasons, models were considerably weaker for *P. brutia* than *P. halepensis* understories, and it appeared as if *P. brutia* was barely regenerating under its currently dense canopy. Additional research is needed to understand the factors influencing understory development in these forests in order to successfully transition to sustainably regenerative systems (Osem et al. 2008).

The need to consider environmental variation, specifically water limitations, when prescribing site-specific management decisions in Israel is highlighted based on the results from this project. Future management decisions should account for the sensitivity to changes in water-availability for *P. halepensis* as well as temperature for *P. brutia.* In addition, the strong variation in understory performance should be taken into account when planning and managing the establishment of the next forest generation. Finally, better documentation of forest management treatments and grazing regimes are required to develop a better understanding the Israel pine forest system.

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APPENDIX

Appendix 1. Correlation coefficient (r) between continuous environmental factors and individual tree and stand level forest parameters for *Pinus halepensis* stands. N = 96

	Diameter	**Density**	**Basal Area**	**NDVI**
Height	0.581***	-0.167	0.279**	0.484***
Diameter		-0.614***	0.023	0.182
Density			0.662***	0.301**
Basal Area				0.437***

* Significant < 0.05
** Significant <0.01
***Significant <0.001

Appendix 2. Correlation coefficient (r) between continuous environmental factors and individual tree and stand level forest parameters for *Pinus brutia* stands. N = 74

	Diameter	**Density**	**Basal Area**	**NDVI**
Height	0.695***	-0.298*	0.349**	0.148
Diameter		-0.588***	0.307**	-0.043
Density			0.492***	0.159
Basal Area				0.159

* Significant < 0.05
** Significant <0.01
***Significant <0.001

Appendix 3. Results of stepwise regression analysis of abiotic factors (explanatory) affecting tree and stand level forest (response) variables in Israel's mature (≥ 32 years) *Pinus halepensis* and *Pinus brutia* forests.

Response	**Explanatory**	**R^2**	**DF**	**EV**	**SS**	**F Ratio**	**Prob > F**
Height$_{Tree}$	Precipitation	0.28	137	0.32	91.34	18.1127	<.0001(+)
	Bedrock				6.81	1.3514	0.2470
	Aspect			0.10	28.92	5.7351	0.0180(S<N)
	Elevation			0.13	38.42	7.6195	0.0066(-)
	Species				10.29	2.0404	0.1554
	Bedrock*Species			0.08	22.79	4.5203	**0.0353**
	Age			0.31	89.84	17.8158	<.0001(-)
Diameter$_{Tree}$	Precipitation	0.26	140	0.19	151.12	10.4080	0.0016(+)
	Elevation				50.13	3.4529	0.0652
	Species			0.12	94.67	6.5200	**0.0117(B<H)**
	Age			0.62	489.86	33.7383	<.0001(-)
MBAI$_{Tree}$	Precipitation	0.11	138	0.50	108.44	13.0148	0.0004(+)
	Elevation			0.14	31.14	3.7381	0.0552(-)
	Species			0.36	79.40	9.5303	**0.0024(B<H)**
Density$_{Stand}$	Precipitation	0.21	138	0.07	1204.00	3.9738	0.0482(-)
	Bedrock			0.09	1443.45	4.7642	0.0307(H<S)
	Elevation			0.30	5118.55	16.8940	<.0001(+)
	Species			0.24	4067.94	13.4264	**0.0004(H<B)**
	Age			0.30	5019.48	16.5670	<.0001(+)
BA$_{Stand}$	Aspect	0.17	136		0.03	0.1518	0.6975
	Elevation			0.24	2.11	9.2261	0.0029(+)
	Species			0.44	3.75	16.4101	<.0001(H<B)
	Aspect*Species			0.13	1.14	4.9777	**0.0273**
	Age				0.18	0.8048	0.3712
	Species*Age			0.16	1.39	6.0965	**0.0148**
NDVI$_{Stand}$	Precipitation	0.26	140	0.34	0.08	17.5193	<.0001(+)
	Aspect			0.14	0.04	7.3319	0.0076(S<N)
	Elevation			0.08	0.02	4.3609	0.0386(+)
	Species			0.43	0.11	22.1316	**<.0001(H<B)**

Appendix 4. Combined *P. halepensis* and *P. brutia* datasets analyzed, using stepwise regression, to investigate species differences in response to abiotic factors.

Response	**Explanatory**	**R^2**	**DF**	**EV[1]**	**SS**	**F Ratio**	**Prob > F**
Pine	Precipitation	0.189	59		927	3.6628	0.0595
	Bedrock				489	1.9294	0.1689
	Species			0.20	1097	4.3327	**0.0408(B<H)**
	Species × Bedrock			0.53	2876	11.3572	**0.0012**
Oak	Precipitation	0.205	62	0.83	6262	22.2147	<.0001
	Basal Area			0.17	1318	4.6747	0.0337
Total	Precipitation	0.252	60	0.80	10874	26.8681	<.0001(+)
	Elevation				1289	3.1857	0.0783
	Basal Area				1419	3.5067	0.0650

[1] EV = Explained variation