

A race to the unknown: Contemporary research on tree and forest drought resistance, an Israeli perspective

Tamir Klein

Department of Plant & Environmental Sciences, Weizmann Institute of Science, 76100, Rehovot, Israel



ARTICLE INFO

Keywords:

Tree physiology
Tree genetics
Forest fluxes
Remote sensing
Forest management

ABSTRACT

Forestry at the dry edge of forest existence has been a long-lasting interest to arid land residents. Current land-use and climate changes have broadened this interest to the global society, seeking for improved tree and forest drought resistance across biomes. Within this transition, Israel is a hub for scientific research and testing ground alike. Israel is a small country, spanning over arid, semi-arid, and thermo-Mediterranean environments, with relatively little forest. Nevertheless afforestation efforts have been unprecedented (by percent change in land cover), and many of these forests serve today as a 'living lab' for forest and tree drought resistance research. Considering the ongoing warming and drying, tree physiologists, forest ecologists, and forest managers in Israel are running a race to the unknown. To ensure local forest sustainability for future generations, the gap between the increased drought risk on the one hand, and the rather stationary forest drought resistance on the other hand, must be closed. The aim of this review is to highlight the findings and achievements, as well as challenges, of this contemporary research. Examples from Israel are given at the Middle East, and the wider, global arid land, contexts. In particular, important progress has been made in the following aspects: (1) the physiology of tree drought resistance, including water-use traits and phenology; (2) the genetic approach, advancing from provenance trials, to the application of molecular tools in the identification of tree drought resistance mechanisms; (3) the canopy flux measurement approach, e.g. monitoring the exchange of carbon, water, and energy in water-limited forests; (4) the application of remote sensing tools, such as satellite-based vegetation indices; and (5) the application of adaptive management practices in increasing forest resilience under drought. Taken together, these advances represent a way forward, while indicating important gaps, and open questions to future research. Lessons learnt in forests in Israel should be useful and transferable to other forest ecosystems in the Middle East, the Mediterranean, and additional water-limited regions.

1. Introduction

Trees are among the most remarkable organisms on planet Earth. Recently, it has been shown that two *Acacia* species of the Middle East actively grow at temperatures as high as 45 °C and relative humidity as low as 6% (Winters et al., 2018). These were single trees growing in desert ephemeral riverbeds. In the slightly wetter conditions of the semi-arid zone, tree communities can already form viable forests. And if forests can sustain in semi-arid sites, then the process of desertification might be attenuated. This was the logic behind the Three Norths Shelterbelt Program in China's northern, semi-arid, frontier; perhaps the world's largest afforestation project in history. In the aftermath of this four-decades-long, million-hectare-wide, program, dust storm occurrence and the rate of desertification were decreased, albeit not at the ratio originally expected (Wang et al., 2010). At the same time, a much smaller afforestation program took place in the Middle East, in the

small country of Israel.

As of the end of 2018, Israel's forests are largely in good condition: most plots seem healthy; forest canopies exchange carbon and water with the atmosphere at expected rates; understory plants increase in biomass and diversity; tree roots grow deeper into the soil; and animals continue to thrive under the shade of the trees. This good condition has been achieved in part by the hard work of the country's forest service, KKL-JNF, and that of the national parks authority; but mostly thanks to the ability of forest trees, of a variety of species, to survive and grow in the dynamic conditions.

In the 17 years that passed since the turn of the millennium, Israel's population increased by 37%, numerous new roads and railways have been built, and urbanization and industry intensified. At the same time, atmospheric changes intensified both locally and globally. Atmospheric CO₂ concentration increased from 377 ppm in 2000 to 403 ppm in 2017, and summers are becoming hotter while winters are becoming

E-mail address: tamir.klein@weizmann.ac.il.

<https://doi.org/10.1016/j.jaridenv.2019.104045>

Received 15 August 2018; Received in revised form 28 March 2019; Accepted 18 October 2019

Available online 25 October 2019

0140-1963/ © 2019 Elsevier Ltd. All rights reserved.

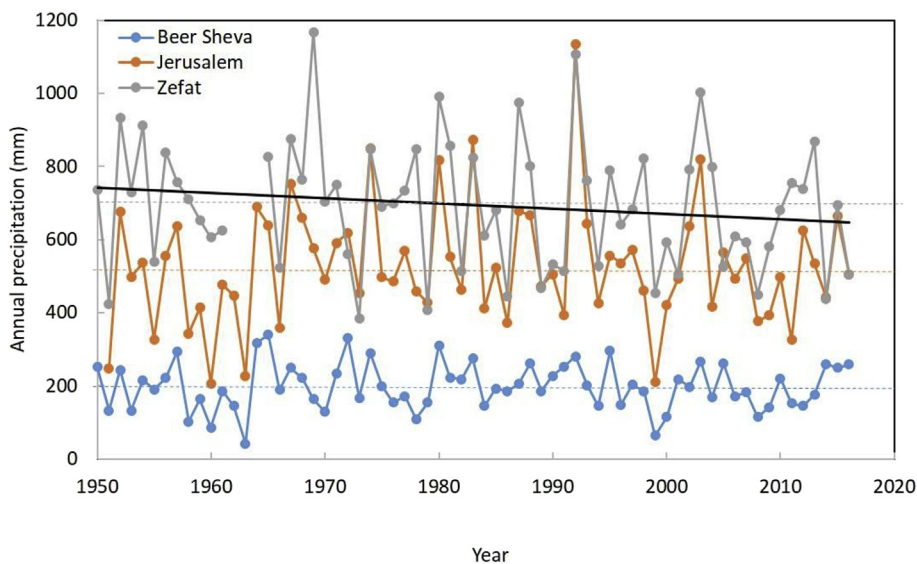


Fig. 1. Forests under increasing water limitation. Changes in annual precipitation for the past seven decades over the three major forest areas in Israel: Beer Sheva (south), Jerusalem (Center), and Zefat (North). Dashed lines represent the long-term mean for each area. A significant long-term drying trend has already been observed in the North (solid line; $P = 0.045$). Data are from the [Israel Meteorological Service report \(2015\)](#) and its database.

milder (IMS report). In the Mediterranean region, including Israel at its southeast corner, precipitation continued to decrease and evaporation continued to increase. Meteorological records for the Middle East show an ongoing warming, predicted to reach a level of $+4\text{ }^{\circ}\text{C}$ by late 21st century (Evans, 2009; Lelieveld et al., 2012). Drying is expected at the north of the region (Turkey, Syria, and Lebanon), and in spite of a mild increase in precipitation predicted for south of the region (e.g. the Arab peninsula), the wet season is becoming shorter (Evans, 2009; Lelieveld et al., 2012). The drought year of 2000 followed the 1999 drought (Fig. 1), and brought upon signs of water stress and even mortality episodes in some forests. The above-average precipitation years of 2002–2004 relieved this long-term stress, but only for a short time: The next years up until 2010 (2013 in the south of Israel) had all below-average precipitation. In fact, only the period of 1958–1963 was drier in the historical meteorological recorded. The second decade of the 21st century had so far some above-average years in the south (2013–2016), but a continued drought in the north, ongoing since 2014 (Fig. 1).

Drought is more than a decrease in annual precipitation. Temporal distribution is key, and moreover in the highly seasonal East Mediterranean, where a 4–6 months long dry season means zero rain for this extended length of time (Raz-Yaseef et al., 2010b). The Mt. Carmel forest fire in 2010, which is the largest forest loss in the history of the state of Israel (~ 1000 ha), serves as an example. The fire erupted, and distributed at unprecedented rate, on the background of one of the driest autumn periods ever recorded. Essentially, this meant a ~ 10 months long dry period. By the time the fire erupted, the forest was so water-depleted, that tree biomass rapidly turned into fuelwood. Pest outbreaks, e.g. that of the Israeli pine bast scale (*Matsucoccus josephi*), can also be regarded as secondary effects of drought, which in turn reduces tree pest resistance mechanisms (Mendel et al., 1997). The *Matsucoccus* epidemic which severely affected > 1400 ha of Mediterranean forest, mostly *Pinus halepensis*, peaked in 1990–1991, following the drought years of 1989–1991, and those of 1984–1987 earlier in the record.

Taken together, climatic trends since 2000 virtually realize the disturbing predictions given earlier for the region (Cohen et al., 2002), with less rainfall, longer dry periods, and more extreme heatwaves. Drought-induced tree mortality has been observed in diffuse patterns in forests across the country, typically affecting $\sim 5\%$ of the trees in each forest (Dorman et al., 2013a). In semi-arid forests in the south, rates were up to 20%. Among species, *Cupressus sempervirens*, *Pinus pinea* and *P. brutia* were typically more sensitive than *Tetraclinis articulata*, *P. canariensis* and *P. halepensis*; Among Eucalypt species, *Eucalyptus occidentalis*, *E. camaldulensis*, and *E. gomphocephala* were more sensitive

than *E. spathulata*, *E. torquata*, and *E. sargentii*. Mortality was also observed outside planted forests, e.g. in *Quercus calliprinos* in maquis in the north (Sever and Neeman, 2008), and in *Acacia raddiana* and *A. tortilis* in the Arava valley (Winters et al., 2015). Much was said and written about the rate of tree adaptation on the one hand, and the rate of climate change on the other (Matyas, 1996). Concern stems from the simple fact that trees, being long-lived organisms, adapt over time-scales of centuries, whereas current climatic changes develop on a decadal time-scale. The current open question is whether tree and forest research can close the gap, offering new ways for sustainable forests under the drying conditions.

The objective of the following review is to provide an Israeli perspective on the major developments in research on forest drought resistance in the 21st century, in the context of global desertification. Naturally, a single paper, as extensive as it may be, cannot provide an exhaustive list covering all research activities. Many important studies, at local to regional scales and from single to multiple species, are not discussed here due to length limitations. Instead, the text focuses on key studies that pushed the field forward, and in some cases conveyed a broader message and consequences outside Israel. In some cases, international contributions which are relevant to forests in Israel are discussed, but the main focus of this review is on research activities in Israel. These contributions are further divided into five categories of forest drought resistance research, described in the respective chapters: (1) tree physiology; (2) tree genetics; (3) forest fluxes; (4) remote sensing of forest; and (5) forest management.

1.1. Forest drought resistance through tree physiology research

The molecular biology revolution in biological research, which started in the 1990s, made numerous breakthroughs in many fields of biology, including the plant sciences. Yet this caused a major shift of resource allocation to genetic and molecular approaches, on expense of the more traditional physiological and anatomical approaches. It was only after a decade or two that the lack of tree physiology research became evident, and a reaction trend started. In fact, contemporary tree physiologists are now being asked to close a ~ 20 -years gap in research of tree structure and function. This call becomes increasingly urgent in face of the existing challenges, and drought stress in particular.

Among tree drought resistance mechanisms, water relations traits are naturally the major subject of study. Improvements to sap flow measurement techniques in the 1990s (Granier and Loustau, 1994; Cermak and Nadezhdina, 1998) enabled the accurate measurement of tree water-use patterns, in both mesic and xeric conditions. Cohen et al.

(2008) measured sap flow in six major forest tree species in Israel and provided the species-specific radial gradient of sap velocity. Although not directly linked to tree drought resistance, this important study proved vital in interpreting sap flow patterns in other studies. In a series of studies, Schiller et al. (2002, 2003, and 2007) reported the water-use patterns of the sclerophyllous broadleaved species *Phillyrea latifolia*, *Quercus calliprinos*, and *Q. ithaburensis*, respectively. With these pioneering sap flow applications, Schiller et al. provided the annual pattern of tree-level and stand-scale water-use for each of the three species, and its response to the long summer drought. In *Quercus calliprinos*, the most important tree species of the local maquis vegetation, water-use persisted throughout the dry season, albeit at sixth of the maximum rate. The annual tree water-use was 44 and 75% of the annual rainfall amount in wet and dry years, respectively (Schiller et al., 2003). Thinning decreased water-use at the stand-scale but increased the tree-level water-use, along with increased growth.

The water-use studies on the sclerophyllous broadleaved species helped understanding their intrinsic drought tolerance. These species are mostly slow-growing, deep-rooted, and anisohydric-like, i.e. their xylem can withstand very negative tensions, e.g. a water potential of -7.0 MPa in the case of *Phillyrea latifolia*. Research on *Pinus halepensis*, the major afforestation tree species, revealed a rather contrasting picture. Klein et al. (2005) showed strong stomatal regulation in this pine species, limiting summer water-use to near-zero amounts in a semi-arid site (Maseyk et al., 2008) and closing stomata at -2.8 MPa (Klein et al., 2011). Such a conservative behavior in a tree should confer higher safety; but not in the drought-vulnerable *P. halepensis*, with 50% loss of xylem hydraulic conductivity already at -3.1 MPa (i.e. a narrow hydraulic safety margin). So what made *P. halepensis* the success story of Israeli afforestation in spite of the recurring drought? Recent research hints to its unique ability to recover embolism in its xylem in yet unprecedented rates of a few hours (Klein et al., 2016). The physiological differences between *P. halepensis* and *Quercus calliprinos*, the two most common tree species in the country, can translate into large effects on the forest water balance and drought resilience (Klein et al., 2013; Fig. 2). Xylem anatomy studies show that these arid-land trees have narrower conduits than their more mesic relatives (David-Schwartz et al., 2016 for *P. halepensis*; Villar-Salvador et al., 1997 for the closely related *Q. coccifera*), with the pine tracheids being typically narrower than the oak vessels. So far, the oak maquis proved more drought-resistant (Klein et al., 2019); but the pine forest uses considerably less water, at higher carbon uptake rates, i.e. it has higher water-use efficiency. Considering the ongoing drying and warming (Lelieveld et al., 2012), the decreased precipitation will not suffice to sustain the oak

maquis (Fig. 2), while extreme droughts might kill more pine trees (Klein et al., 2019).

The science of wood anatomy originally stemmed from the more traditional field of dendrochronology. Tree-rings, being a natural archive of tree-climate interactions, are still a powerful tool in the quest for improved tree drought resistance. Essentially, the strong forcing exerted by the limited precipitation facilitates interpretation of tree-ring data from the arid zone (Klein et al., 2005; Touchan et al., 2008; Dorman et al., 2013a). Plotting tree-ring widths against precipitation dynamics for *Juniperus phoenicia*, *Pinus halepensis*, and *Quercus aegilops* from Jordan yielded useful correlations (Touchan and Hughes, 1999). In turn, these correlations permitted climate reconstructions for the last four centuries, highlighting climate variability in periods that preceded meteorological measurements. A similar approach applied on dendrochronologies from Tunisia, identified the past conditions arid forests endured, including drought years in the 19th century (Touchan et al., 2008). Looking closer to identify intra-ring growth dynamics can provide more information on species' eco-physiology. In Israel, the use of tree-ring carbon isotope composition as an index for water-use efficiency was validated this way (Klein et al., 2005); and cambial activity was deciphered for the desert tree *Prosopis flexuosa* in an arid Patagonia woodland (Giantomasi et al., 2012). Recently, dendrochronologies are being used to identify and predict tree mortality risks on a local scale in Israel (Dorman et al., 2013a) and on the global scale (Cailleret et al., 2018). The latter meta-analysis found that a gradual growth decline and an increase in inter-annual growth variability can be used as early-warning signals of drought-induced mortality in gymnosperm species.

Tree drought resistance mechanisms go far beyond water relations. For example, Maseyk et al. (2008) noted a decoupling between stem and needle growth phenologies in *P. halepensis*: stem growth followed the wet season and adjusted to the local winter conditions, counter-intuitively forming the coolest growth season across Europe (Rotenberg and Yakir, 2010), whereas needle growth was still occurring throughout the long dry season. This meant that needle length serves as a good proxy for drought stress in this species (Klein et al., 2014a), but also raised a fundamental question about growth at very low assimilation rates. A tree-scale carbon balance revealed that carbon storage in late winter was crucial for subsidizing needle growth in summer (Klein and Hoch, 2015). Such detailed information is crucial to understand how forests in Israel will respond to future conditions. For example, higher temperatures in the dry season could exacerbate drought stress, but in the wet season they might enhance growth; and a shorter wet season can be more detrimental to trees than a below-average rainfall year (Raz-Yaseef et al., 2010a).

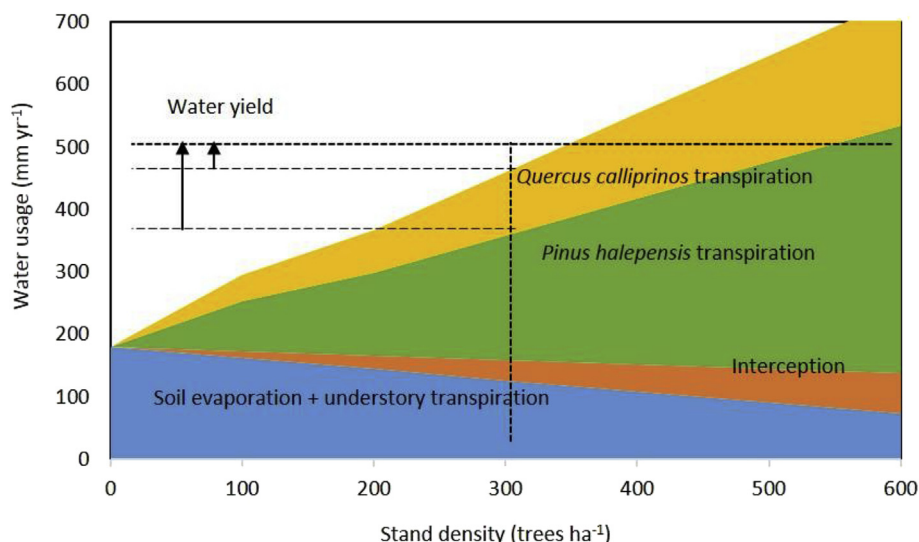


Fig. 2. Oak/pine differences in water-use translate to higher scales. Expected changes in the partitioning between hydrological flux components in response to stand density changes for a *Pinus halepensis* forest and a *Quercus calliprinos* maquis. The increasingly higher stand-level transpiration amount in an oak vs. pine stand comes on expense of the water yield. At typical stand density of 300 trees ha^{-1} and annual precipitation of 500 mm (vertical and horizontal dotted lines, respectively), the water use of *P. halepensis* and a *Q. calliprinos* stands are expected to be 357 and 459 mm (long dash lines), leaving 143 and 41 mm as water yield, respectively (arrows). Such analysis also indicates the carrying capacity for the different stands (e.g., ~ 350 and ~ 550 trees ha^{-1} for oak and pine at 500 mm year^{-1}). Adapted from Klein et al. 2013.

1.2. Tree genetics for forest drought resistance

The fact that certain tree genotypes can perform better under drought than others, makes the genetic approach very appealing to forest management programs. The first steps in this direction were at the ecotype, rather than the genotype level. The case of the pan-Mediterranean *P. halepensis* provenance trials shows nicely how this research field developed along the past two decades. Originally, Israel joined the UN FAO program on *P. halepensis* seed collection provenance trials from across the Mediterranean, contributing two provenances (Elkosh and Shachariya) and the field trials in Beit Dagan, Yatir forest, and a few other sites. Schiller et al. (1986) were the first to study allele frequencies in certain loci, showing relatively little variation, and a western/eastern population subdivision. Analysis of genomic DNA and protein polymorphism in local populations showed an increase in the percent of polymorphic loci, from 12% to 48%, with site dryness (Korol et al., 2002). This study further showed how the peripheral population in Yatir forest is under selection pressure that eliminates homozygous and favors heterozygous genome, in turn highlighting the role of plasticity in tree drought resistance. Phenotypic differentiation became evident as provenance trials matured, showing the higher performance of certain Greek provenances and the higher drought resistance of local vs. foreign populations (Atzmon et al., 2004; Schiller and Atzmon, 2009). Using the same trials, Klein et al. (2012) provided the physiological context to these observations, showing higher xylem vulnerability to embolism in provenances from Italy and Algeria, compared to those from Greece and Israel, in turn with higher growth rate or higher water-use efficiency, respectively. The inferiority of the provenances from Italy and Algeria can relate to the wetter, or, cooler, conditions at their sites of origin, respectively (Voltas et al., 2018), as well as to their lower heterozygosity (Korol et al., 2002).

The *P. halepensis* provenance research did not stop there. Israeli forest scientists, in collaboration with international experts, continued using this template to facilitate genotype selection for future afforestation from the one hand, and to improve our understanding of underlying mechanisms on the other hand. Up until 2016 it was clear that xylem resistance to embolism is the key to tree drought tolerance, but it was still unknown what the xylem structures underlying this tolerance were exactly. In coniferous xylem, water flows through narrow and short tracheids through membrane-equipped pits, called torus and margo, respectively. Studying the xylem anatomy of the exact same trees of the same provenances, it was found that those vulnerable provenances from Italy and Algeria had significantly lower overlap between the torus and pit aperture, compared to those from Greece and Israel (David-Schwartz et al., 2016). Essentially, this meant higher torus margo closing pressure in the latter provenances. A single thread connects the anatomical observations (David-Schwartz et al., 2016) to the physiological measurements (Klein et al., 2012), and the field observations showing differential survival rates of the exact same four provenances (Schiller and Atzmon, 2009; Fig. 3). Taken together, these results highlight the strength of continuous, interdisciplinary research on tree drought resistance in Israel.

In many ways, the aforementioned molecular biology revolution skipped the field of forest tree research. Indeed, forest trees present multiple objective challenges to molecular techniques: due to their relatively slow growth rate and maturation, transformation and propagation techniques are more complex in forest trees; and the fact that conifers have the largest known genomes among all living organisms is another caveat. Yet local, contemporary research seems to finally take on some of these challenges. Recently, the *P. halepensis* drought needle transcriptome has been constructed (Fox et al., 2017). This elaborate project opens the gate to detailed research of numerous gene candidates in multiple biochemical pathways. A good place to start would be the key structural processes identified in past physiological research of tree drought response, such as carbohydrate metabolism, aquaporin channel activity, cell wall suberization, endodermis and exodermis structure,

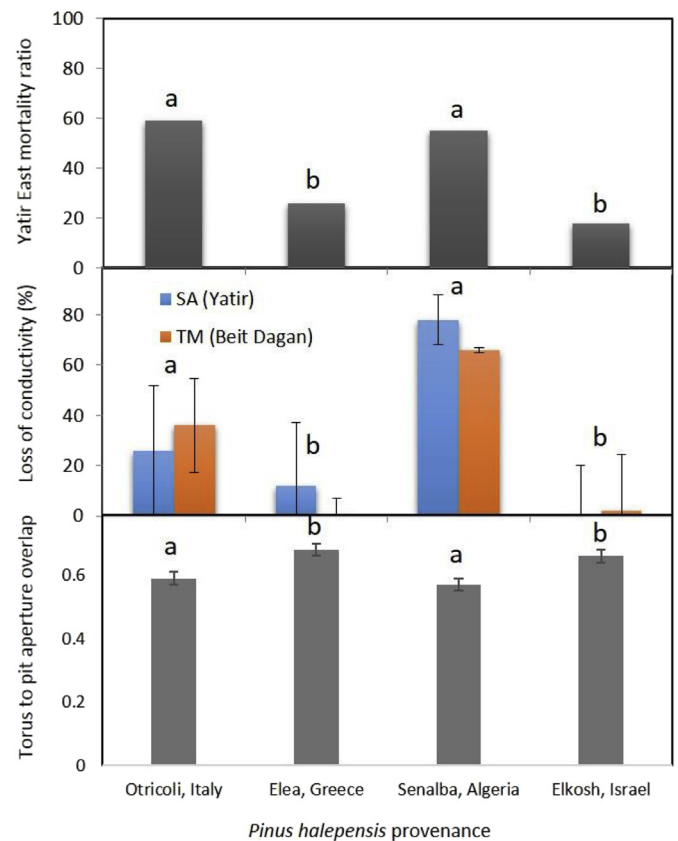


Fig. 3. The power of interdisciplinary approach in tree drought resistance research. The higher drought-induced mortality ratio of the Italian and Algerian Aleppo pine provenances, vs. the Israeli and the Greek, observed by Schiller and Atzmon (2009; top) had a physiological basis of higher sensitivity to embolism (Klein et al., 2013; middle). Embolism level was provenance-specific across semi-arid (SA) and Thermo-Mediterranean (TM) sites. In turn, the higher sensitivity was explained by lower torus to pit aperture overlap in the xylem (David-Schwartz et al., 2016).

xylogenesis, differential above- and belowground growth, and others (Schwinning and Ehleringer, 2001; Maseda and Fernández, 2006). In addition, the molecular approach holds the potential to expose novel, yet unknown pathways. By identifying the major cellular players in drought-exposed trees, we are gradually improving our understanding of the underlying mechanisms in tree drought resistance.

1.3. Forest fluxes under drought

Obviously, a forest is more than the sum of its trees. One of the major advances in recent research on forest drought resistance in Israel is in the quantification of major forest fluxes. These fluxes are involved in biogeochemical cycling of elements (e.g. carbon, nitrogen) or compounds (water), and their monitoring is largely facilitated by recent improvements in micro-meteorological techniques. The implementation of eddy-covariance, infra-red gas analysis, and isotopic analysis in forests in Israel marked the transition from classical forest ecology to forest flux biogeochemistry, and much of it has been directed toward the research of forest drought resistance. The call to use the southernmost pine afforestation at Yatir (Korol et al., 2002) as a field-based laboratory for forest function under drought was well received, and a 17 m flux tower was constructed there in the year 2000 (Fig. 4). Yatir forest is among the driest canopy-forming forests worldwide, with leaf area index of ~1.5 at annual precipitation of 285 mm (Sprintsins et al., 2011). The role of the flux tower at Yatir goes far beyond local or regional interest, as it represents a vast global area of semi-arid forests



Fig. 4. Studying forest drought resistance at the frontier of the dry timberline. Yatir forest in 2010: The flux tower over the forest canopy (top); Diffuse Aleppo pine mortality (middle); And a near-empty water reservoir, the result of prolonged drought, highlighting the forest role in the local water balance. Photos' credits: Tamir Klein, Emanuela Negreanu.

(Rotenberg and Yakir, 2010). Over the years, major fluxes have been measured onsite, exposing multiple ecosystem-level processes of drought resistance.

Constructing the hydrological balance of a forest is prerequisite for the evaluation of its drought resistance. Research in Yatir forest along the past two decades demonstrates the fast evolution of research capabilities, which followed the technological advances, from sap-flow (Schiller and Cohen, 1998) to soil evaporation and ecosystem evapotranspiration (Raz-Yaseef et al., 2010a,b) and soil hydrology (Klein et al., 2014b). The remarkable precipitation-use efficiency of the semi-arid forest, with > 90% of the rainfall cycling to evapotranspiration, and ~60% of the rainfall transpired by trees, was the first discovery (Schiller and Cohen, 1998, Raz-Yaseef et al., 2010a,b, Ungar et al., 2013, Klein et al., 2014b). Focusing on the interplay between canopy cover (a function of stand density), soil evaporation, and tree transpiration, has already identified an upper limit to stand density under the low water budget (Raz-Yaseef et al., 2010a). Further work highlighted the role of rainwater input rate, showing that rain storms were more effective for forest water availability than a higher number of smaller rain events (Raz-Yaseef et al., 2010b). In that sense, climate extremes such as rain storms might compensate for an overall drying conditions forecasted for the region. Deeper analysis of the soil structure in Yatir exposed the role of a clay-rich layer, at 0.5 m belowground, in holding the water above it (Klein et al., 2014b). Accurately quantifying the soil water dynamics allowed for prediction of tree drought stress, including the observed mortality in 2009 (Fig. 3). In a sense, this approach extends on the earlier study of bedrock as a major site quality parameter, showing higher pine performance on marl and chalk >

dolomite > limestone (Schiller, 1982).

Forests are a major component in the carbon cycle, and their drought resistance interacts with their ability to store carbon, while continuously receiving more anthropogenic CO₂ from the atmosphere. Using the eddy-covariance methodology on top of the Yatir flux tower, Grünzweig et al. (2003) have shown an unexpectedly high carbon sequestration rates of ~0.2 kg C m⁻² yr⁻¹, in line with the rates measured over temperate forests.

This single observation was a revolution by itself, replacing our previous view of local forests being a poor fraction of the 'real' forests from higher latitudes, and emphasizing the vast potential of semi-arid forests within the global carbon cycle and climate system (Rotenberg and Yakir, 2010). In addition, we learnt that forests in Israel are already adapting to the long-term drought conditions in a way that disqualifies measurements of temperate forest response to drought episodes as a model (Grünzweig et al., 2009; Klein et al., 2014c). Which factors contributed to the observed enhanced carbon storage following afforestation? Field measurements, complemented by isotopic and decomposition experiments, indicated high soil organic carbon accumulation (Grünzweig et al., 2007) and high belowground carbon allocation, accounting for ~40% of canopy CO₂ uptake (Grünzweig et al., 2009). Unexpectedly, this enhanced carbon storage was at otherwise unchanged soil nitrogen concentration (Grünzweig et al., 2007). This high nitrogen use efficiency might be related to high synchronization between nitrate availability and tree activity in the wet season, in turn benefiting from attenuated nitrate production from ammonia oxidation (Gelfand and Yakir, 2008). Clearly, abiotic and biotic rhizosphere processes hold great potential for further improving forest drought resistance in Israel and beyond.

Despite of its many discoveries, the flux approach to forest drought resistance is far from realizing its full potential. As measurements in the atmosphere and soil intensify, more focused research becomes available. As one example, focusing on short heatwave periods, Tatarinov et al. (2016) managed to decouple the effects of soil and atmospheric drought on the semi-arid pine forest. Forest carbon and water vapor exchanges showed a strong response to air dryness, that weakened as soil moisture decreased. The large (~60%) decreases in carbon exchange and canopy conductivity to water vapor during a heatwave, typically recovered to pre-stress levels within a single day, demonstrating the high ecosystem plasticity and resilience to drought (Tatarinov et al., 2016). The rich datasets coming from flux measurements are also a gold mine for eco-physiological and eco-hydrological measurement and modeling (Fig. 5). Incorporation of such models in predicting forest response to drought has already helped upscaling spatial measurements (Klein et al., 2014b), and should intensify in the near future. Two of the best candidate sites for integrating a modeling approach are the stand density experiments in Kdoshim and Yatir forests. These thinning and grazing experiments are not only large-scale but also long-term and consistent in monitoring procedures, under the long-term ecological research (LTER) framework. These field manipulations hold great promise for sustainable forestry under climate change.

2. Forest drought resistance: results from remote sensing

When studying vegetation patterns over large areas, such as in forests, remote sensing tools become increasingly important. The ongoing increase in the diversity and resolution of sensors on the one hand, and in the ability to analyze and synthesize their output, also using models, on the other hand, means a more intensive utility in future research. Aerial photography of forest has been used in the past in Israel, and should produce important data on forest drought resistance in coming years. It is satellite imaging, however, that has recently made a scientific breakthrough in local forest research. Using Landsat satellite images for 1994–2011, Dorman et al. (2013a,b) estimated forest performance under drought across Israel by the normalized difference

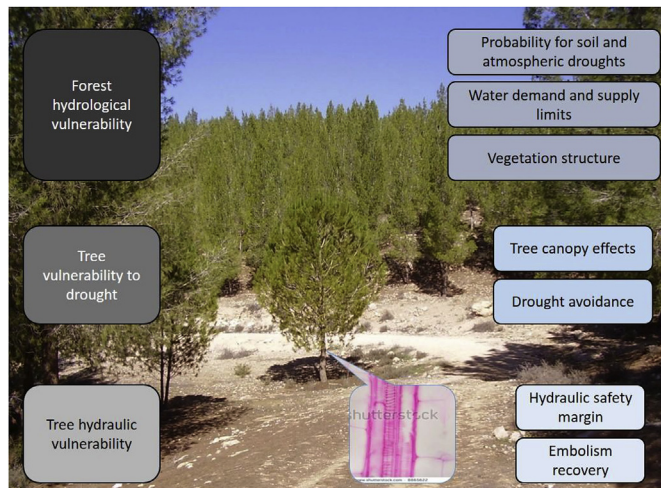


Fig. 5. The multiple scales of forest drought vulnerability. Conceptual framework for advanced assessment of forest drought vulnerability. Such assessment integrates species-specific hydraulic and drought-acclimation data with responses and ways to build resilience at the forest scale.

vegetation index (NDVI). Forests in the south, at the dry timberline, were more affected than those in central Israel (mostly west of Jerusalem), which nevertheless had higher sensitivity to precipitation than forests both south and north of them (Dorman et al., 2013a). Locally, higher performance in northern vs. southern aspects was observed in wet years but not in drought years (Dorman et al., 2013b). The integration of NDVI data with tree-ring chronologies (Dorman et al., 2013a) proved powerful in a follow-up study focused on drought-induced tree mortality (Dorman et al., 2015a,b). The diffuse tree mortality in Lahav and Dvira, two dry timberline forests, was higher in older-aged sparse stands, on southern aspects, and on deeper soils. These patterns exposed the high complexity in deciphering mortality risks, as well as taking measures to reduce such risks, e.g. the benefits of forest thinning.

The potential of remote sensing goes beyond the NDVI. Recently, additional satellite data have been utilized together with meteorological data and advanced modeling approaches. Using the enhanced vegetation index (EVI) combined with NDVI derived from the moderate-resolution imaging spectrometer (MODIS) onboard the Terra satellite, it was shown that water yield ranged from 48% to 8% of precipitation in local humid and dry forests, respectively (Helman et al., 2017a). In addition, the drier forests showed higher hydrological resilience to drought than the more humid forests. One of the strengths of that national-scale analysis was that many of its 36 predefined forest areas were dominated by *Pinus pinea* and *Pinus brutia* rather than the more common *P. halepensis*, though no significant species effect was observed. Next, a similar interdisciplinary methodology was applied in a comparative study of the *P. halepensis* forest and the oak (*Quercus calliprinos*) maquis on Mt. Carmel (Helman et al., 2017b). The remote sensing approach confirmed the upscaling of eco-physiological measurements showing higher water-use efficiency and lower water-use of pine vs. oak (Klein et al., 2013; Fig. 2). Last, this analysis predicted reductions of 16% in the productivity of both forests, for projected increase in mean temperature of 1 °C, as result of global warming.

3. Forest management for improved forest drought resistance

The recent drought effects on forests, and the 2010 Carmel fire aftermath, echoed in the Israeli forest management community, bringing together forest scientists (Osem et al., 2011) and forest managers (Porat et al., 2017). One of the results of this collaborative work was the creation of a forest management code (Osem et al., 2013) and its adoption by the national forest service KKL, with guidelines for

application (Porat et al., 2017). The risks involved in an Aleppo pine monoculture approach were already known, including high flammability (Carmel et al., 2009) and pest vulnerability (Mendel et al., 1997). For this reason, Osem et al. (2009) tested the potential of transforming existing plantations into mixed Mediterranean forests through natural regeneration, indicating large differences based on the local water availability (see also Sheffer, 2012). The large drought-induced forest loss in the Carmel fire was a major catalyst pushing for a change in existing practice. Prescribed thinning and grazing, together with conservation of the maquis vegetation, and delineation of safety fire belts, were among the chief aftermath recommendations (Perevolotski et al., 2011). Traditionally, grazing in semi-arid woodlands has been associated with land degradation and soil erosion (as in the Greek island of Crete; Hill et al., 1998). The removal of forest understory plants and tree litter by heavy grazing affects ecosystem processes from carbon sequestration (Nosetto et al., 2006) to insect community composition (Molina et al., 1999). Yet these effects appear more complex than previously thought, with soil organic carbon and root carbon virtually unaffected by grazing (Nosetto et al., 2006). Instead, controlled grazing becomes an important management tool in semi-arid forests.

The national masterplan 22 for forest and afforestation, which was signed in 2006, laid the foundation for a forest management code (Osem et al., 2013). Many of the principles of this code, including the facilitation of sustainability and adaptive management (Osem et al., 2008, 2011), were designed to increase the drought resistance of the forest. How did these principles translate into management practices? Porat et al. (2017) describe the planning of thinning and grazing applications in Kdoshim forest as an example. Where possible, tree pruning is yet another management option. In a dryland woodland in Sudan, pruning of *Prosopis juliflora* trees increased their leaf production by 60% and improved their hydraulic status (Elfadl & Luukkanen 2003). Drought-induced tree mortality can mark the end of a forest, but careful planning can help creating a more sustainable forest at the same site. State-and-transition models are one of the tools to test management alternatives prior to their application in the field (Cobb et al., 2017). Last, the value of continuous monitoring, which was acknowledged in the code, facilitated the establishment of a national network of 80 monitoring plots (Sprintsin et al., 2014). These plots, which are independent from the periodical forest inventory surveys, will provide more information on drought stress and its forest response. Monitoring of tree health should be further improved with the adoption of the standards of the European forest monitoring network (ICP Forests; www.icp-forests.org).

4. Synthesis and future perspectives

Tree physiologists, forest ecologists, and forest managers across arid environments, and in Israel in particular, are running a race to the unknown. To ensure local forest sustainability for future generations, the gap between the increased drought risk on the one hand, and the rather stationary forest drought resistance on the other hand, must be closed. This review paper opened with two, rather contrasting, national arid land afforestation programs: China's Three Norths Shelterbelt (Wang et al., 2010), and Israel's greening program (Osem et al., 2011). For many good reasons, both projects should be highlighted also outside of their locations. Nevertheless, much of the scientific knowledge available today was missing at the time these projects started. What made China's arid afforestation less successful than anticipated? This investigation is ongoing. What made Israel's afforestation sensitive to prolonged drought and fire? Recent research from the local, regional, and global scientific community provides some clues. Among the messages conveyed in this review, it is clear that: (1) seed and plant material were sub-optimal in many cases. Today, provenance and species selection are supported by current research; (2) forest management practices such as thinning and grazing have not been fully

implemented. Field experiments now confirm their role in ensuring forest sustainability; and (3) forestry data management relied on the traditional inventory surveys. With the remote sensing tools and Geographical Information System currently available, forest management is much improved. Still, arid land forests in Israel, and other places, have been highly successful in sequestering carbon, channeling it to long-term storage in the soil. In many cases, this was achieved with little effect on the water yield, which is so important in arid environments. The contemporary research reviewed here highlights the following points:

1. New tools such as transcriptomics and forest tree transformation open the gate to the discovery of new drought-response genes. A molecular approach should be promoted, but unlike many examples with annual plants, it must be accompanied with an eco-physiological approach. The roles of tree aquaporins and carbohydrate metabolism enzymes in regulating hydraulic conductivity and carbon storage, respectively, are already under investigation.
2. The rhizosphere of arid land forests is still largely unexplored, and holds great potential to the future of forests under drought. Root processes such as soil water exploration, carbon storage, and exudation, can be more important for tree drought resistance than aboveground processes. Also, more research should be dedicated to identifying local mycorrhiza species and quantifying their role in increasing water supply to trees.
3. Forest thinning, pruning and grazing practices are already being applied in many sites. Yet, more research is needed to test their impact on forest drought resistance. This considers the observation of drought-induced tree mortality across multiple stand densities.
4. New remote sensing tools, from drones to satellites, will become increasingly critical in forest drought resistance research. As new sensors provide novel spectral products at ever-increasing spatial and temporal resolutions, precious data accumulate and await analysis. Indeed, remote sensing tools are incomplete without analytical capabilities to match. These should be further complemented by ground observations. For example, the KKL GIS maps will introduce a new layer, entirely dedicated to tree mortality reporting.
5. The Mediterranean maquis ecosystem, which has shown higher drought resistance than the coexisting conifer forest, attracted far less research so far. Nevertheless, under the new forest management code, this vegetation type, along with a mixed conifer-broadleaved forest, will become increasingly important. Its higher drought resistance is encouraging, yet a tipping-point scenario should not be ruled out (Sever and Neeman, 2008).

Copyright statement

All the materials included in this review are with the author.

Declaration of competing interest

The authors declare no competing financial interests.

Acknowledgements

The author wish to thank the Merle S. Cahn Foundation and the Monroe and Marjorie Burk Fund for Alternative Energy Studies; Mr. and Mrs. Norman Reiser, together with the Weizmann Center for New Scientists; The KKL-JNF Israel Forest Service; The Israel-US BSF grant "Using water potential of soils and plants as a unifying term to assess forest vulnerability to drought"; The Weizmann Sustainability and Alternative Energy Research Initiative; The Yeda-Sela Center for Basic Research; The Angel Faivovich Foundation for Ecological Research; and the Edith & Nathan Goldberg Career Development Chair. The paper benefitted from useful comments on an earlier version, made by an anonymous reviewer.

References

- Atzmon, N., Moshe, Y., Schiller, G., 2004. Ecophysiological response to severe drought in *Pinus halepensis* Mill. trees of two provenances. *Plant Ecol.* 171 (1), 15–22.
- Cailleret, M., Dakos, V., Jansen, S., Robert, E.M., Aakala, T., Amoroso, M.M., et al., 2018. Early-warning signals of individual tree mortality based on annual radial growth. *Front. Plant Sci.* 9, 1964.
- Carmel, Y., Paz, S., Jahashan, F., Shoshany, M., 2009. Assessing fire risk using Monte Carlo simulations of fire spread. *For. Ecol. Manag.* 257 (1), 370–377.
- Cermak, J., Nadezhkina, N., 1998. Sapwood as the scaling parameter-defining according to xylem water content or radial pattern of sap flow? In: *Annales des Sciences forestieres*, vol 55. EDP Sciences, pp. 509–521 No. 5.
- Cobb, R.C., Ruthrof, K.X., Breshears, D.D., Lloret, F., Aakala, T., Adams, H.D., Hartmann, H., 2017. Ecosystem dynamics and management after forest die-off: a global synthesis with conceptual state-and-transition models. *Ecosphere* 8 (12), e02034.
- Cohen, S., Ianetz, A., Stanhill, G., 2002. Evaporative climate changes at bet dagan, Israel, 1964–1998. *Agric. For. Meteorol.* 111 (2), 83–91.
- Cohen, Y., Cohen, S., Cantuarias-Aviles, T., Schiller, G., 2008. Variations in the radial gradient of sap velocity in trunks of forest and fruit trees. *Plant Soil* 305 (1–2), 49–59.
- David-Schwartz, R., Paudel, I., Mizrahi, M., Delzon, S., Cochard, H., Lukyanov, V., et al., 2016. Indirect evidence for genetic differentiation in vulnerability to embolism in *Pinus halepensis*. *Front. Plant Sci.* 7.
- Dorman, M., Perevolotsky, A., Sarris, D., Svoray, T., 2015a. The effect of rainfall and competition intensity on forest response to drought: lessons learned from a dry extreme. *Oecologia* 177 (4), 1025–1038.
- Dorman, M., Svoray, T., Perevolotsky, A., 2013a. Homogenization in forest performance across an environmental gradient—The interplay between rainfall and topographic aspect. *For. Ecol. Manag.* 310, 256–266.
- Dorman, M., Svoray, T., Perevolotsky, A., Sarris, D., 2013b. Forest performance during two consecutive drought periods: diverging long-term trends and short-term responses along a climatic gradient. *For. Ecol. Manag.* 310, 1–9.
- Dorman, M., Svoray, T., Perevolotsky, A., Moshe, Y., Sarris, D., 2015b. What determines tree mortality in dry environments? a multi-perspective approach. *Ecol. Appl.* 25 (4), 1054–1071.
- Elfadl, M.A., Luukkanen, O., 2003. Effect of pruning on *Prosopis juliflora*: considerations for tropical dryland agroforestry. *J. Arid Environ.* 53 (4), 441–455.
- Evans, J.P., 2009. 21st century climate change in the Middle East. *Clim. Change* 92 (3–4), 417–432.
- Fox, H., Doron-Faigenboim, A., Kelly, G., Bourstein, R., Attia, Z., Zhou, J., et al., 2017. Transcriptome analysis of *Pinus halepensis* under drought stress and during recovery. *Tree Physiol.* 1–19.
- Gelfand, I., Yakir, D., 2008. Influence of nitrite accumulation in association with seasonal patterns and mineralization of soil nitrogen in a semi-arid pine forest. *Soil Biol. Biochem.* 40 (2), 415–424.
- Giantomasi, M.A., Roig-Juñent, F., Patón-Domínguez, D., Massaccesi, G., 2012. Environmental modulation of the seasonal cambial activity in *Prosopis flexuosa* DC trees from the Monte woodlands of Argentina. *J. Arid Environ.* 76, 17–22.
- Granier, A., Loustau, D., 1994. Measuring and modelling the transpiration of a maritime pine canopy from sap-flow data. *Agric. For. Meteorol.* 71 (1–2), 61–81.
- Grünzweig, J.M., Gelfand, I., Yakir, D., 2007. Biogeochemical factors contributing to enhanced carbon storage following afforestation of a semi-arid shrubland. *Biogeosci. Discuss.* 4 (4), 2111–2145.
- Grünzweig, J.M., Hemming, D., Maseyk, K., Lin, T., Rotenberg, E., Raz-Yaseef, N., et al., 2009. Water limitation to soil CO₂ efflux in a pine forest at the semiarid "timberline". *J. Geophys. Res.: Biogeosciences* 114 (G3).
- Grünzweig, J.M., Lin, T., Rotenberg, E., Schwartz, A., Yakir, D., 2003. Carbon sequestration in arid-land forest. *Glob. Chang. Biol.* 9 (5), 791–799.
- Helman, D., Lensky, I.M., Yakir, D., Osem, Y., 2017a. Forests growing under dry conditions have higher hydrological resilience to drought than do more humid forests. *Glob. Chang. Biol.* 23 (7), 2801–2817.
- Helman, D., Osem, Y., Yakir, D., Lensky, I.M., 2017b. Relationships between climate, topography, water use and productivity in two key Mediterranean forest types with different water-use strategies. *Agric. For. Meteorol.* 232, 319–330.
- Hill, J., Hostert, P., Tsiourlis, G., Kasapidis, P., Udelhoven, T., Diemer, C., 1998. Monitoring 20 years of increased grazing impact on the Greek island of Crete with earth observation satellites. *J. Arid Environ.* 39 (2), 165–178.
- Israel Meteorological Service report, 2015. Climate Change in Israel.
- Klein, T., Hoch, G., 2015. Tree carbon allocation dynamics determined using a carbon mass balance approach. *New Phytol.* 205 (1), 147–159.
- Klein, T., Cahanovitch, R., Sprints, M., Herr, N., Schiller, G., 2019. A nation-wide analysis of tree mortality under climate change: forest loss and its causes in Israel 1948–2017. *For. Ecol. Manag.* 432, 840–849.
- Klein, T., Cohen, S., Yakir, D., 2011. Hydraulic adjustments underlying drought resistance of *Pinus halepensis*. *Tree Physiol.* 31 (6), 637–648.
- Klein, T., Cohen, S., Paudel, I., Preisler, Y., Rotenberg, E., Yakir, D., 2016. Diurnal dynamics of water transport, storage and hydraulic conductivity in pine trees under seasonal drought. *iFor. Biogeosci.* 9 (5), 710.
- Klein, T., Di Matteo, G., Rotenberg, E., Cohen, S., Yakir, D., 2012. Differential ecophysiological response of a major Mediterranean pine species across a climatic gradient. *Tree Physiol.* 33 (1), 26–36.
- Klein, T., Hemming, D., Lin, T., Grünzweig, J.M., Maseyk, K., Rotenberg, E., Yakir, D., 2005. Association between tree-ring and needle δ¹³C and leaf gas exchange in *Pinus halepensis* under semi-arid conditions. *Oecologia* 144 (1), 45–54.
- Klein, T., Hoch, G., Yakir, D., Körner, C., 2014a. Drought stress, growth and nonstructural carbohydrate dynamics of pine trees in a semi-arid forest. *Tree Physiol.* 34 (9),

- 981–992.
- Klein, T., Rotenberg, E., Cohen-Hilaleh, E., Raz-Yaseef, N., Tatarinov, F., Preisler, Y., et al., 2014b. Quantifying transpirable soil water and its relations to tree water use dynamics in a water-limited pine forest. *Ecohydrology* 7 (2), 409–419.
- Klein, T., Shpringer, I., Fikler, B., Elbaz, G., Cohen, S., Yakir, D., 2013. Relationships between stomatal regulation, water-use, and water-use efficiency of two coexisting key Mediterranean tree species. *For. Ecol. Manag.* 302, 34–42.
- Klein, T., Yakir, D., Buchmann, N., Grünzweig, J.M., 2014c. Towards an advanced assessment of the hydrological vulnerability of forests to climate change-induced drought. *New Phytol.* 201 (3), 712–716.
- Korol, L., Shklar, G., Schiller, G., 2002. Genetic variation within *Pinus halepensis* Mill. provenances growing in different microenvironments in Israel. *Isr. J. Plant Sci.* 50 (2), 135–143.
- Lelieveld, J., Hadjinicolaou, P., Kostopoulou, E., Chenoweth, J., El Maayar, M., Giannakopoulos, C., et al., 2012. Climate change and impacts in the eastern mediterranean and the Middle East. *Clim. Change* 114 (3–4), 667–687.
- Maseda, P.H., Fernández, R.J., 2006. Stay wet or else: three ways in which plants can adjust hydraulically to their environment. *J. Exp. Bot.* 57 (15), 3963–3977.
- Maseyk, K.S., Lin, T., Rotenberg, E., Grünzweig, J.M., Schwartz, A., Yakir, D., 2008. Physiology–phenology interactions in a productive semi-arid pine forest. *New Phytol.* 178 (3), 603–616.
- Matyas, C., 1996. Climatic adaptation of trees: rediscovering provenance tests. *Euphytica* 92 (1), 45–54.
- Mendel, Z., Assael, F., Saphir, N., Zehavi, A., Nestel, D., Schiller, G., 1997. Seedling mortality in regeneration of Aleppo pine following fire and attack by the scale insect *Matsucoccus josephi*. *Int. J. Wildland Fire* 7 (4), 327–333.
- Molina, S.I., Valladares, G.R., Gardner, S., Cabido, M.R., 1999. The effects of logging and grazing on the insect community associated with a semi-arid chaco forest in central Argentina. *J. Arid Environ.* 42 (1), 29–42.
- Nosetto, M.D., Jobbágy, E.G., Paruelo, J.M., 2006. Carbon sequestration in semi-arid rangelands: comparison of *Pinus ponderosa* plantations and grazing exclusion in NW Patagonia. *J. Arid Environ.* 67 (1), 142–156.
- Osem, Y., Brand, D., Tauber, I., Perevolotski, Tzoref, H., 2013. Israel's forest management code – policy and guideline to forest planning. *Ecol. Environ.* 4, 129–130.
- Osem, Y., Ginsberg, P., Tauber, I., Atzmon, N., Perevolotsky, A., 2008. Sustainable management of Mediterranean planted coniferous forests: an Israeli definition. *J. For.* 106 (1), 38–46.
- Osem, Y., Mendel, Z., Neeman, G., Perevolotski, A., Riou, Y., Shiller, G., 2011. The planted Mediterranean conifer forest in Israel: discussion of management principles. *Ecol. Environ.* 1, 224–228.
- Osem, Y., Zangy, E., Bney-Moshe, E., Moshe, Y., Karni, N., Nisan, Y., 2009. The potential of transforming simple structured pine plantations into mixed Mediterranean forests through natural regeneration along a rainfall gradient. *For. Ecol. Manag.* 259 (1), 14–23.
- Perevolotski, A., Boneh, O., Zalutski, M., Lahav, H., Kaplan, D., Snir, H., Steiner, N., 2011. Extract of the recommendation report of the committee for Carmel forest management and restoration. *Ecol. Environ.* 2, 169–171.
- Porat, Y., Tsoret, H., Osem, Y., 2017. A forest masterplan as a planning tool for objective-oriented forest management – the case of Kdoshim forest. *Ecol. Environ.* 8, 50–56.
- Raz-Yaseef, N., Rotenberg, E., Yakir, D., 2010a. Effects of spatial variations in soil evaporation caused by tree shading on water flux partitioning in a semi-arid pine forest. *Agric. For. Meteorol.* 150 (3), 454–462.
- Raz-Yaseef, N., Yakir, D., Rotenberg, E., Schiller, G., Cohen, S., 2010b. Ecohydrology of a semi-arid forest: partitioning among water balance components and its implications for predicted precipitation changes. *Ecohydrology* 3 (2), 143–154.
- Rotenberg, E., Yakir, D., 2010. Contribution of semi-arid forests to the climate system. *Science* 327 (5964), 451–454.
- Schiller, G., 1982. Significance of bedrock as a site factor for Aleppo pine. *For. Ecol. Manag.* 4 (3), 213–223.
- Schiller, G., Atzmon, N., 2009. Performance of Aleppo pine (*Pinus halepensis*) provenances grown at the edge of the Negev desert: a review. *J. Arid Environ.* 73 (12), 1051–1057.
- Schiller, G., Cohen, Y., 1998. Water balance of *Pinus halepensis* Mill. afforestation in an arid region. *For. Ecol. Manag.* 105 (1), 121–128.
- Schiller, G., Cohen, S., Ungar, E.D., Moshe, Y., Herr, N., 2007. Estimating water use of sclerophyllous species under East-Mediterranean climate: III. Tabor oak forest sap flow distribution and transpiration. *For. Ecol. Manag.* 238 (1), 147–155.
- Schiller, G., Conkle, M.T., Grunwald, C., 1986. Local differentiation among Mediterranean populations of Aleppo pine in their isoenzymes. *Silvae Genet.* 35 (1), 11–19.
- Schiller, G., Ungar, E.D., Cohen, Y., 2002. Estimating the water use of a sclerophyllous species under an East-Mediterranean climate: I. Response of transpiration of *Phillyrea latifolia* L. to site factors. *For. Ecol. Manag.* 170 (1), 117–126.
- Schiller, G., Ungar, E.D., Moshe, Y., Cohen, S., Cohen, Y., 2003. Estimating water use by sclerophyllous species under east Mediterranean climate: II. The transpiration of *Quercus calliprinos* Webb. in response to silvicultural treatments. *For. Ecol. Manag.* 179 (1), 483–495.
- Schwinning, S., Ehleringer, J.R., 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *J. Ecol.* 89 (3), 464–480.
- Sever, N., Neeman, G., 2008. Desiccation and recovery of *Quercus calliprinos* in Israel following consecutive drought years. *Yaar* 10, 10–16.
- Sheffer, E., 2012. A review of the development of Mediterranean pine–oak ecosystems after land abandonment and afforestation: are they novel ecosystems? *Ann. For. Sci.* 69 (4), 429–443.
- Spritsin, M., Cohen, S., Maseyk, K., Rotenberg, E., Grünzweig, J., Karnieli, A., et al., 2011. Long term and seasonal courses of leaf area index in a semi-arid forest plantation. *Agric. For. Meteorol.* 151 (5), 565–574.
- Spritsin, M., Danysuk, J., Mor, I., Guanin, J., Wilson, T., Osem, Y., 2014. The establishment of long-term monitoring system in mature pine forests. *Ecol. Environ.* 5, 68–70.
- Tatarinov, F., Rotenberg, E., Maseyk, K., Ogée, J., Klein, T., Yakir, D., 2016. Resilience to seasonal heat wave episodes in a Mediterranean pine forest. *New Phytol.* 210 (2), 485–496.
- Touchan, R., Hughes, M.K., 1999. Dendrochronology in Jordan. *J. Arid Environ.* 42 (4), 291–303.
- Touchan, R., Meko, D.M., Aloui, A., 2008. Precipitation reconstruction for Northwestern Tunisia from tree rings. *J. Arid Environ.* 72 (10), 1887–1896.
- Ungar, E.D., Rotenberg, E., Raz-Yaseef, N., Cohen, S., Yakir, D., Schiller, G., 2013. Transpiration and annual water balance of Aleppo pine in a semiarid region: implications for forest management. *For. Ecol. Manag.* 298, 39–51.
- Villar-Salvador, P., Castro-Díez, P., Pérez-Rontomé, C., Montserrat-Martí, G., 1997. Stem xylem features in three *Quercus* (Fagaceae) species along a climatic gradient in NE Spain. *Trees (Berl.)* 12 (2), 90–96.
- Volts, J., Shestakova, T.A., Patsiou, T., Di Matteo, G., Klein, T., 2018. Ecotypic variation and stability in growth performance of the thermophilic conifer *Pinus halepensis* across the Mediterranean basin. *For. Ecol. Manag.* 424, 205–215.
- Wang, X.M., Zhang, C.X., Hasi, E., Dong, Z.B., 2010. Has the Three Norths Forest Shelterbelt Program solved the desertification and dust storm problems in arid and semiarid China? *J. Arid Environ.* 74 (1), 13–22.
- Winters, G., Otieno, D., Cohen, S., Bogner, C., Ragowloski, G., Paudel, I., Klein, T., 2018. Tree growth and water-use in hyper-arid *Acacia* occurs during the hottest and driest season. *Oecologia* 188 (3), 695–705.
- Winters, G., Ryykin, I., Rudkov, T., Moreno, Z., Furman, A., 2015. Mapping underground layers in the super arid Gidron Wadi using electrical resistivity tomography (ERT). *J. Arid Environ.* 121, 79–83.