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Age, rainfall and gender expression in stressed *Pinus pinea* trees planted in an arid region

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A B S T R A C T

Gender expression of 145 individually marked *Pinus pinea* trees planted in the arid transition zone between the Mediterranean district and the Negev Desert in Israel was recorded for thirteen consecutive years (1988–2000), from the age of nine to twenty-one. Like several other young Mediterranean conifers, *P. pinea* trees frequently change their gender expression. On average, each tree expressed 5.2 gender situations during those 13 years. The proportion of all reproducing trees, and monoecious as well as female to male ratio, followed the changes in annual rainfall in the first eight flowering years. Three unusually rainy El Niño years (1988, 1992, 1995), two years that followed a rainy El Niño year, and a regular rainy year, considerably increased the trees' monoeciousness in the population. The young trees began their reproduction as males, and about half of them gradually became monoecious. This trend, which is typical also for *P. pinea* trees growing in humid habitats, ceased at the age of 17 years, when drought, combined with strong competition over water in a stand that should have undergone two essential thinning treatments that were not done, totally suppressed the female allocation and only some maleness remained. Maleness as a stress response can be used as a tool for forest management, especially when deciding on essential thinning. The above reflects a highly adjustable phenotypic plasticity in resource allocation to reproduction, which seems to be advantageous mainly in both young and physiologically weak small trees on the one hand, and in stressed older ones on the other.

1. Introduction

Pinus pinea L., the Italian stone pine, is the only Mediterranean piñon pine. Its natural distribution is unknown because of its millennia-long use as a fruit and timber tree around the Mediterranean basin (Mirov, 1967; Kislev, 1988; Pereira et al., 2015). *Pinus pinea*'s very narrow genetic variability (e.g., Soto et al., 2010) indicates a very small founder population. The annual rhythm of cambial activity of young *P. pinea* plants, with winter dormancy in young specimens, seems to indicate an origin in high mountains or in a cool northern Mediterranean region frozen in winter (Liphschitz et al., 1984; Liphschitz and Lev-Yadun, 1986). *Pinus pinea* is known to respond strongly to water availability. Water availability was found to influence growth-ring width and structure in *P. pinea* trees growing in several countries and climatic conditions: Italy (Cherubini, 1993), Turkey (Akkemik, 2000), Spain (Mutke et al., 2003), and Portugal (Campelo et al., 2006). Similarly, the amount of ripe female cones in mature commercial *P. pinea* plantations in Italy (Pozzera, 1959), Chile (Loewe-Muñoz et al., 2016), and female flowering in grafted seed orchards in Spain (Mutke et al., 2003, 2005a), was positively influenced by higher rainfall. *Pinus pinea* has huge seeds (666 mg) compared with other Mediterranean pines, such as *P. halepensis*, which has seeds of 19 mg (Tapias et al., 2004). Moreover, they have a thick woody

seed coat and large, woody, heavy, and costly mature female cones. In mature trees growing in southern France, 21.5% of the tree's productivity was allocated to reproduction, out of which 92.5% was directed to female cones, and only 7.5% to male cones (Rapp and Cabanettes, 1981). In general, allocation to female cones in *P. pinea* trees is similar to the allocation to the trunk's wood production (Mutke et al., 2005b). The female component thus comprises the major part of the reproductive effort, and is comparable to the major vegetative growth effort of *P. pinea* trees. As such, it is expected to respond to changing environmental conditions.

Typical Mediterranean conifers including *P. pinea* usually considered to be monoecious, such as *Cupressus sempervirens* (Lev-Yadun and Liphschitz, 1987), *Pinus halepensis* and *P. brutia* (Panetsos, 1981; Shmida et al., 2000; Ne'eman et al., 2011), begin their reproductive years as females and gradually become monoecious, with a tendency toward maleness under stress conditions (Lev-Yadun and Liphschitz, 1987; Shmida et al., 2000). Similarly, the basically monoecious Mediterranean conifer tree *Juniperus phoenicea* has female, male and monoecious individuals that may change their gender from year to year at a different frequency in various populations (Jordano, 1991). Gender changes of individual trees are also common in *C. sempervirens* (Lev-Yadun and Liphschitz, 1987), and in *P. halepensis* (Shmida et al., 2000). *Pinus pinea* and *P. pinaster* are two Mediterranean conifers that express maleness in their early reproductive years and only gradually become monoecious (Shmida et al., 2000; Santos-del-Blanco et al., 2012). In this respect, *P. pinea* is similar to the American piñon pine *P. edulis*, which also starts reproduction as a male (Floyd, 1983). As in all pines and in many other conifers, clusters of male cones are formed on the lower and somewhat older branches of the canopy, and female cones are usually formed in new branches or in new branch parts on higher parts of the canopy in *P. pinea* (Shmida et al., 2000), a character considered to lower selfing (Longman, in Veillon, 1978; Shmida et al., 2000). In *C. sempervirens*, for instance, since female cones are formed on new extension growth and male cones on older branches, aridity stress, which reduces extension growth results in increased or in total maleness (Lev-Yadun and Liphschitz, 1987).

The El Niño phenomenon is the outcome of warming of a huge block of water in the Pacific Ocean. The release of this enormous energy budget results in extreme storms in South America. After the excess energy stored in the Pacific Ocean's water is released in the storms, the relevant huge block of water becomes cooler, resulting in the La Niña phenomenon that lasts longer than than the El Niño phase (Philander, 1990). Many studies have demonstrated the influence of El Niño events on ecosystems and the biology of individual species (e.g., Wooster and Fluharty, 1985; Glynn, 1988; Diaz and Markgraf, 1992; Holmgren et al., 2001). At the heart of the El Niño-affected zones, flowering is greatly influenced by El Niño and La Niña cycling, in some of the regions following increased rainfall, and in some following droughts (Curran et al., 1999; Wright et al., 1999). Naturally, El Niño effects in Israel are much less evident than in the Pacific or in America. However, even in areas quite remote from El Niño's origin, such as the arid region of Israel, El Niño years, with their considerably higher rainfall, evidently have dramatic effects on plant growth and reproduction. Since the mid-1970s, there has usually been more than average rainfall in Israel during El Niño years (Yakir et al., 1996; Price et al., 1998). In *P. halepensis* trees growing west of Jerusalem (Israel), the increase in annual rainfall during El Niño years resulted in the production of wider growth rings also characterized by a strong climatic signal in the stable isotopes of the wood (Yakir et al., 1996). Other botanical effects of El Niño years were not studied in the region.

As part of a long-term effort to study the ontogeny of gender and the influence of environmental variables on gender changes in eastern-Mediterranean conifers, I monitored gender expression of *P. pinea* trees in a planted forest in the Mediterranean-desert transition zone for thirteen consecutive years. Here I describe trees' gender ontogeny with age under stressing arid conditions, and the effects of variation in rainfall on its gender expression.

2. Materials and methods

The flowering patterns and responses of the *P. pinea* trees presented here should be viewed according to the basic responses of the other conifer tree taxa of that forest, planted at the edge of the desert. The small forest, which was planted in the year 1980 in loess soil, at Lehavim (34°48'E; 31°22'N), 14 km north of Be'er-Sheva, included adjacent almost monospecific groves of five conifers: *Pinus brutia*, *P. canariensis*, *P. halepensis*, *P. pinea*, and *Cupressus sempervirens*. The site is located in the transition zone between the Mediterranean district and the Negev Desert. The average annual rainfall during the 13 study years was 304.8 mm, ranging from 135 to 525 mm. The rainfall data (Table 1) are from a nearby station (Lehavim, two km south-east of the studied plot), generously provided by the Meteorological service. Decades of earlier rainfall measurements indicated that the long-term average annual rainfall there is 260–270 mm (Precipitation Map, 1987). The years 1988, 1992, 1995, 1998 were El Niño years, all of which except for 1998, had more than

average rainfall in Lehavim. However, 1998 was very rainy in the northern parts of Israel.

Table 1: Gender expression in *Pinus pinea* and annual rainfall at Lehavim

Year	Male trees	Female trees	Monoecious trees	Not flowering	Total femaleness	Total no. of trees	Annual rainfall mm
1988*	66	7	19	53	26	145	370
1989	82	3	24	36	27	145	275
1990	119	0	14	11	14	144	300
1991	127	0	3	14	3	144	399
1992*	69	0	71	4	71	144	525
1993	101	0	34	9	34	144	311
1994	103	0	0	41	0	144	263
1995*	66	4	55	18	59	143	423
1996	121	0	0	22	0	143	249
1997	104	0	0	38	0	142	266
1998*	90	0	0	52	0	142	281
1999	57	0	0	85	0	142	135
2000	45	0	0	96	0	141	166
Total	1,150	14	220	479	234		

Total femaleness = females + monoecious. * El Niño years.

Unfortunately, the trees were not thinned by the forest authorities in order to balance between the limited available soil water amounts at that arid site, and those required for the photosynthetic biomass that grew and grew every year. Except for *P. canariensis* and *P. halepensis*, which expressed milder morphological responses to the water shortage, the other three conifer species suffered severely from the lack of water, as was obvious from their morphology and growth in the beginning and their decline and death in later years. According to my unpublished field notes, many of the *P. pinea* trees resumed the production of juvenile needles in their southern side of the canopy, a stress response that can usually be found in dwarfed or very stressed *P. pinea* trees in more humid habitats in Israel. The *P. brutia* grove was the first to show severe irrepareable damage and decline because of the limited water supply. It included a very dramatic loss of most of their needles, reduced and later arrested reproduction, very low rates of cambial activity and radial growth, and ended by the premature death of many trees in the late 1990s. The *C. sempervirens* grove was the second to show severe damages, and many of the trees died. The *P. halepensis* grove suffered much less, and several *P. halepensis* trees that grew among the *P. brutia* trees remained green, their canopy was densely packed with green needles, and they grew much taller and wider than the *P. brutia* that stood only several meters away, and could thus be easily distinguished from the *P. brutia* trees from a distance of more than half a kilometer. The *P. canariensis* and *P. halepensis* groves still exist today at age 40, and the *P. pinea* grove continued to decline so much after I finished my measurements, that all the *P. pinea* trees were cut down by the forestry authorities several years later. It was clear to me that the forest had to be thinned in order to dramatically reduce competition and to leave a density in the range of 50% of the planted density in the groves of the more drought-tolerant pines (*P. canariensis* and *P. halepensis*), to thin the sensitive species (*P. brutia*, *P. pinea* and *C. sempervirens*) to 50% of the original density not later than at age 10–12 years, and five years later, to repeat such a thinning. The fact that trees sensitive to arid conditions were not thinned, doomed the groves of the three less drought hardy species to severe obvious decline and with time, to death (see Lorimer, 1980, 1985; Cailleret at al., 2019; Klein et al., 2019; Preisler et al., 2019; Tsamir et al., 2019). The forest was re-planted by other species after the non-thinned plots collapsed, a waste of a significant sum of public money, and a loss of potential shaded recreation and rest spots at the edge of the desert.

In the year 1988, when the *P. pinea* trees were nine years old, 145 trees growing in four parallel rows were marked individually. In each row, the first 35–37 trees were marked, beginning in the western edge of the rows. Of these marked trees, four died during the study. Gender expression of each tree was recorded every year at the time of new cone production in the spring during thirteen consecutive years (1988–2000).

3. Results

Maleness was more common than any other gender type in 12 of the 13 years (Table 1; Fig. 1). Altogether, male flowering alone occurred 1,150 times, non-flowering 479 times, monoecy 220 times, and female alone 14 times (Table 1). The year 1992, which was the rainiest year in Israel in the last century, was the only year with more trees forming female cones than those forming strictly male ones (71 monoecious trees and 69 male trees). During the last five years of the study, all flowering trees were males, but in the last two years, there were more non-flowering trees than male trees. Only 14 strictly female flowering trees were found, and all during three out of the 13 years. Two of these years (1988 and 1995) were El Niño years, and one year (1989) was a year after an El Niño year. Monoecious trees occurred in seven of the years (Table 1; Fig. 1). Three of them (1988, 1992, 1995) were very rainy El Niño years, two of them (1989, 1993) were the years after a very rainy El Niño year, and the year 1991 was very rainy irrespective of El Niño. Rainfall levels during el-Niño years were significantly higher than rainfall levels during regular years (Wilcoxon rank-sum test, $W = 4$, $p = 0.016$). The

peaks in the number of monoecious trees occurred in 1989 (a year after an El Niño year) and in 1992 and 1995, two El Niño years (Table 1). In two of the four El Niño years (1992, 1995) the total femaleness (female and monoecious) showed a clear peak in expression, while the number of strictly male individuals was greatly reduced (Table 1; Fig. 1). Rainfall, all of which occurs during late autumn, winter and spring, had a significant effect on the sexual allocation and gender expression of the trees in the spring. The proportion of reproductive trees and of monoecious trees to total trees, as well as the proportion of female functioning trees (monoecious and females) to male trees, followed the fluctuations in the annual rain amount till the trees were 17 years old (Table 1; Fig. 1). There was a strong trend toward cessation of flowering in the last years of the study, which were drier than usual. Several sequent droughts, combined with competition over water in a stand that should have undergone two essential thinning treatments that were not done, totally suppressed the female allocation and only some maleness remained.

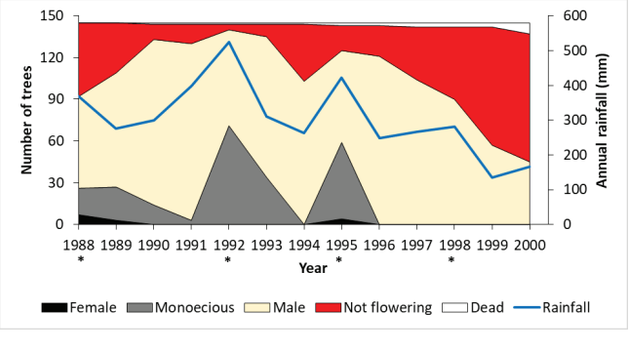

Figure 1: Gender expression in the *Pinus pinea* population planted at Lehavim and its relation to rainfall. El Niño years are marked with an asterisk

Most trees changed their gender several times. Only four trees kept the same gender throughout the study. Twelve trees expressed two gender situations, 16 trees three gender situations, 17 trees four gender situations, 27 trees five gender situations, 27 trees six gender situations, 26 trees seven gender situations, 12 trees eight gender situations and four trees nine gender situations. On average, each tree expressed 5.2 gender situations during the 13 years. The various gender situations of the four trees that had nine gender situations are shown in Table 2. After the year 2000, the trees' vigour declined dramatically, and several years later the whole population was cut down by the forestry authorities.

Table 2: *Pinus pinea* trees at Lehavim expressing nine gender situations in 13 years

Gender situation	Tree 1	Tree 2	Tree 3	Tree 4
1	not flowering	male	not flowering	monoecious
2	male	monoecious	male	male
3	not flowering	male	monoecious	monoecious
4	male	not flowering	male	male
5	not flowering	monoecious	monoecious	monoecious
6	male	male	male	male
7	not flowering	monoecious	monoecious	monoecious
8	male	male	male	male
9	not flowering	not flowering	not flowering	not flowering

4. Discussion

Gender change is a well-known phenomenon in pine trees. Dozens of *Pinus* species are already known to gradually change gender with age, as part of their normal ontogeny (Righter, 1939; Floyd, 1983; Shmida et al., 2000; Kang, 2007; Ne'eman et al., 2011; Santos-del-Blanco et al., 2012). While about 15 pine species are known to start reproduction as males (Righter, 1939; Floyd, 1983; Shmida et al., 2000; Santos-del-Blanco et al., 2012), about 30 pine species are known to start their reproduction as females (Righter, 1939; Panetsos, 1981; Floyd, 1983; Shmida et al., 2000; Ne'eman et al., 2011). Righter (1939) found that out of the 55 pine species he studied, 18 started reproduction as monoecious, 23 as females, and 12 as males. In *P. johannis* the majority of the trees are unisexual, i.e., this pine species from the Sierra Madre Oriental (Mexico) is almost dioecious (Flores-Rentería et al., 2013). The gender ontogeny of about half of the species of the genus *Pinus* is still unknown. However, even in the better studied species, the full repertoire of gender changes has never been studied. Several pine species were found to change gender to male in response to various stress conditions. Stressed mature *P. flexilis* trees growing at timberline of the Rocky Mountain National Park in Colorado (USA) were males or did not flower at all (Kiener, 1935). The same is true for *P. montana* trees growing near the timberline of the Alps in Switzerland (Schroeter, 1926, cited by Kiener, 1935). Two piñon pines, i.e., low and stressed *P. culminicola* trees growing near timberline in Mount Cerro Potosí in Mexico, and *P. cembroides* trees growing near timberline in the Chiricahua Mountains in Arizona, are commonly males or don't flower at all, but some of the trees in those mostly male populations are monoecious (McCormick and Andersen, 1963). In dense populations of *P. contorta*, growing under conditions

of strong competition, the trees had a narrow but tall canopy, and their relative allocation to male cones was higher than to female ones. In *P. contorta* trees that grew without competition far from neighbours, the canopy was much shorter and much wider. In such trees, the relative allocation to female cones was much higher (Smith, 1981). Under arid conditions, the youngest trees of the piñon pine *P. edulis* were males, slightly older ones were females, and only mature ones were monoecious (Floyd, 1983). Following chronic herbivory by moths, mature *P. edulis* trees were either males, or did not form any cones (Whitham and Mopper, 1985). Stressed and slow growing trees of *P. densiflora* growing in Korea tended to be males (Kang, 2007). The results presented here show that *P. pinea*, growing in very dry conditions compared to typical Mediterranean ones, tends to form only male cones, or to stop reproduction altogether under increasing water stress, which is in accordance with the common tendency of plants in general (Freeman et al., 1980, 1981; Charnov, 1982) and in conifers, including pines, in particular (e.g., Kiener, 1935; McCormick and Andersen, 1963; Floyd, 1983; Whitham and Mopper, 1985; Lev-Yadun and Liphschitz, 1987; Shmida et al., 2000) to become males. The high resource allocation to female flowering in *P. pinea* (Rapp and Cabanettes, 1981), and the large size of seeds and female cones of this species (Tapias et al., 2004), probably contributed to the evolution of allocating only to the male function at young age, and to the expression of phenotypic plasticity with a strong tendency to express maleness under stress in mature trees.

The data presented here demonstrate the positive effects of higher than usual annual winter rainfall on the subsequent allocation to the female function. Many *P. pinea* trees in the studied population changed their gender in response to various amounts of rainfall. The trees alternated between non-reproduction and male under very dry conditions, and between bisexual (monoecious) and male under more humid ones. This reflects a highly adjustable phenotypic plasticity in resource allocation to reproduction, which seems to be advantageous mainly in both young and physiologically weak small trees on the one hand, and in stressed older ones on the other.

Pinus pinea trees respond to competition and drought by reducing growth and reproduction even under more humid Mediterranean conditions (Gonçalves et al., 2017; Loewe-Muñoz et al., 2019, 2020). In more arid habitats, the various responses of the trees to water shortage and competition are naturally more pronounced. Since this pattern of gender flexibility is especially important in arid conditions, and is in accordance to the amount of available water resources, enhanced maleness may be used as a rule of thumb, i.e., as a marker for significant stress in pine stands that should be taken care of, for instance by thinning and branch prunning in order to reduce competition and stress. The gender responses to water stress shown here can thus be used as a management tool for *P. pinea* forests and plantation. When the proportion of trees forming female cones declines, thinning should be performed. The same is true for several other Mediterranean pines. When the trees continue to be stressed and reach the stage of showing severe needle loss, it seems to be too late to treat the trees by traditional mild forestry methods such as thinning and pruning, and irrigation might then become essential, something that is not feasible in most cases of large-scale forest management.

The effects of El Niño in the eastern Mediterranean region were found not so long ago (Yakir et al., 1996; Price et al., 1998), and have been obvious only for some 45 years, since the 1970's, probably as a result of global warming. Thus, little has been done to shed light on its local biological effects. El Niño teleconnections, which increase rainfall in the eastern Mediterranean in certain years, so very far from its origin in the Pacific Ocean, can thus influence gender expression and reproduction in a Mediterranean conifer such as *P. pinea*. However, these effects are only part of a complicated pattern of the phenotypic plasticity in sexual allocation in *P. pinea* in accordance with the amount of annual winter rainfall. The observed changes in *P. pinea* growth and reproduction described here probably reflect other, still unknown components of the influence of the El Niño and La Niña phenomena on our local biota. This should be studied in the future.

Two different reasons seem to account for femaleness being especially pronounced in three (1988, 1992, 1995) of the four El Niño years, and not at all in the last El Niño year (1998). In the first El Niño year, the trees were still young, at the age when in *P. pinea* trees maleness dominates as a regular ontogenetic pattern (Shmida et al., 2000). Therefore, the enhanced femaleness was weaker than in the following two El Niño years. The 1998 El Niño year was not as rainy in southern Israel as it had been in several previous El Niño years (although it was very rainy in the north), and the trees that had already suffered three sequential drought years (Table 1; Fig. 1), and were in general in the process of a strong decline in vitality, produced only male cones or did not flower at all.

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