

Mediterranean Stone Pine: Botany and Horticulture

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ABSTRACT

The seeds of Mediterranean stone pine, *Pinus pinea*, have been consumed by humans since the Paleolithic era. Similarly to edible seeds from other Eurasian or American pines, Mediterranean pine nuts and cones assumed early cultural, symbolic, and spiritual attributes by local cultures. They were represented in Neolithic rock paintings and sacred in the ancient high cultures, especially relevant in Greco-Roman cults. Although stone pine is well known and has been planted since antiquity, pine nuts still are gathered mainly in natural forests, and only recently has the crop taken the first steps from wild harvested to

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Stone pine is a good candidate for conversion to a horticultural crop. Its pine nuts are among the most expensive nuts, whose high price has made them an attractive opportunity as alternative crop on rain-fed farmland in Mediterranean climates. The species performs well on poor soils and needs reduced cultural practices in comparison with alternative crops, it is affected by few pests or diseases, and it resists climate adversities such as drought and extreme or late frosts. The current knowledge about stone pine as a plantation nut crop in specific plantations is still limited. At shoot level, vegetative and reproductive vigor are associated in the same axes. This imposes an “expanding crown” ideotype that limits the potential selection of highly productive dwarf cultivars for a modern, intensive, high-density horticultural system. The managed grafted trials with selected genotypes indicate that productivity of the forest land where these are located can be increased several-fold in comparison with yields in traditional stone pine forests. The stone pine has potential as a crop in agroforestry systems; in tree lines, such as shelterbelts adjacent to farmland or pastures; or in proper low-density orchard plantations. The ongoing standardization of the processing and the finished product might extend its use as a crop in Mediterranean climate zones around the world.

KEYWORDS: agroforestry; conifer seeds; domestication; pine breeding; *Pinus pinea*

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I. INTRODUCTION

A. Natural and Cultural History

Mediterranean stone pine, *Pinus pinea* L. (Pinaceae), is one of the most characteristic tree species of the Mediterranean landscape because of its singular umbrella shape and the ancient use of its large, nutlike edible seeds for human consumption. Some of the common names are derived from these two characteristics: Mediterranean or Italian stone pine, umbrella pine, pin pignon or pin parasol (French), and pino piñonero (Spanish). Other names reflect its ancient cultural history: pino domestico (Italian), pino doncel (Spanish), pinheiro manso (Portuguese), and *Pinus domestica* or *P. sativa* (Latin). Theophrastos and Dioscorides, who both wrote in Greek, called it peuke (peykh), either as peuke emeron $\frac{1}{4}$ tame pine or peuke konophoron $\frac{1}{4}$ cone-bearing pine, distinguishing it from other pines denominated generally as pí'tys (petyV) (Gil 2008). The Latin name *pinus* was used by classical authors exclusively in reference to *P. pinea* and has been extended to other species only since the botanical writings of Albertus Magnus in the Middle Ages (Mirov 1967). Stone pine is a widespread tree of Mediterranean forests and woodlands, and it has been exploited since the Paleolithic era for its edible seed (Badal 2001; Finlayson et al. 2006). Adapted to dry environments, stone pine forests are important for watershed and soil protection, especially stabilizing dunes, and in terms of biodiversity, constituting habitats for some endangered species, such as the Iberian lynx, Iberian imperial eagle, black vulture, peregrine falcon, and black stork

(!etal.1999).Anotherprominentfeatureofthisspeciesinthe Mediterraneanlandscapeisitspresenceasisolatedtrees,increeksand roadside tree lines, or in small rural groves. These are structural elements of the landscape, interrupting the uniformity and large expanse of cereal farmland with evergreen tree islands, and thus play an important ecological role providing food, refuge, and passageways for many animal species, especially for birds (SEO/BirdLife 1999).

Mediterranean stone pine is also a horticultural tree, cultivated for ornamental purposes, shade, and the seeds since antiquity. Virgil's *Bucolics* states: "fraxinus in silvis pulcherrima, pinus in hortis, populus in fluviis, abies in montibus altis" (fairest is the ash in the forest, the pine in the garden, the poplar by the stream, the fir on the mountain-heights). Although this tree is native or at least a protohistoric archeophyte in most Mediterranean countries, it is said to have been "cultivated" since the Neolithic or "since at least 6,000 years" (Earle 2009). However, little effort seems to have been made for its proper domestication as a nut crop. There are no defined cultivars, and nearly all the current stone pine nut production is still harvested from wild stands, where no cultivation techniques are applied except for silvicultural practices that regulate stand composition and density. Even the small pine groves or isolated border trees, so typical of Mediterranean rural landscapes, are normally seed-grown without known pedigree. Thus, stone pine is basically a wild-collected species. Only in the last decades have increasing efforts been dedicated to clonal selection with production in grafted orchards (Prada et al. 1997; Mutke et al. 2000b).

If stored dry, the hard-shelled pine nuts are durable for many years without losing the capacity to germinate. Germination is easy and epigenous, and the lack of inbreeding depression (Ammannati 1989) allows new local populations to establish from a few fallen seeds without any negative founder effects. Once established either intentionally or accidentally in a suitable site, the robustness and phenotypic plasticity of the stone pine allow it to persist and spread over wider areas, disseminated by rodents or birds (dyszoochory) (Rejmánek and Richardson 2003). Thus, the long-distance seed transfers since prehistory does not necessarily imply an intentional cultivation in a silvicultural or even horticultural sense (Mutke et al. 2007a).

The stone pine industry is not based on any known cultivar but on trees from unselected seeds, a condition that might be related to the extremely low genetic diversity found in the species (Vendramin et al. 2008). Only one botanical variety has been described, mentioned by Pliny the Elder in *Historia Naturalis* (Book XV) as *tarentina*, "the shell of which may be broken with the fingers and hence it becomes a prey to

"#birdswhilestillonthetree."ThisprobablyreferstoPinuspineaavar. fragilisDuhamel,whichproducessoft-shelledseeds,arecessive Mendelian trait, which is the result of a single chromosomal mutation (Macchia 1974). It can occur spontaneously and has been found independently several times in different forests in Italy and Spain. However, it lacks commercial interest for three reasons: (1) its seeds are smaller than normal and often empty, (2) due to preharvesting predation, and (3) due to low durability in storage (Ammannati 1989; Agrimi and Ciancio 1993; Fady et al. 2004).

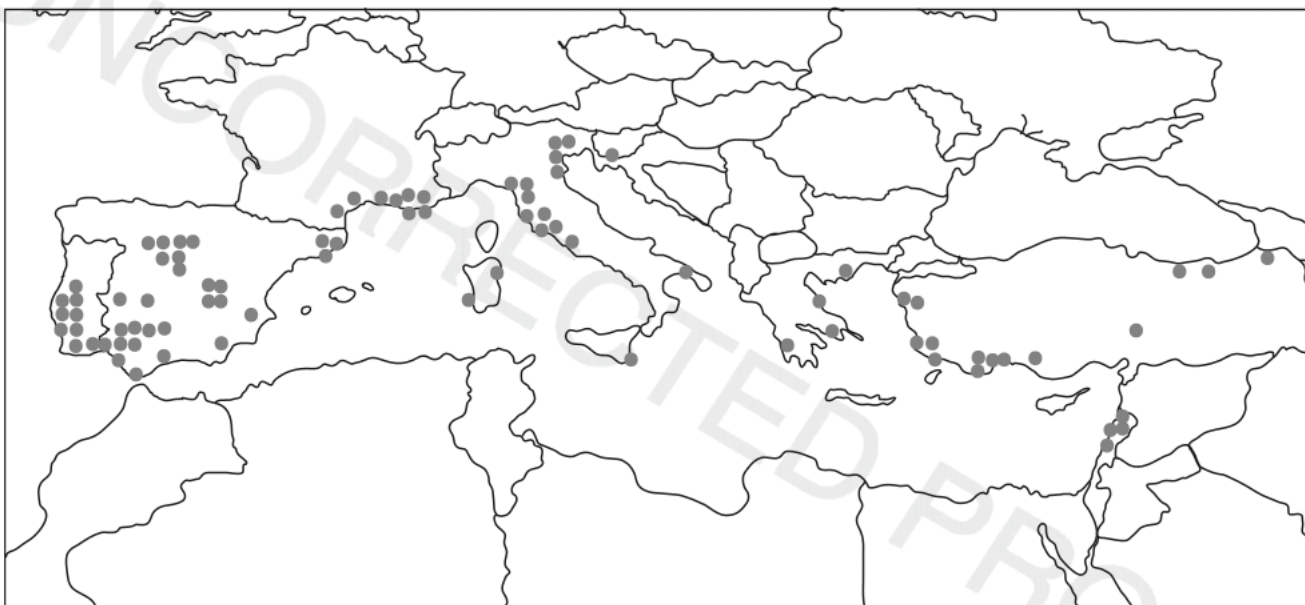
Since antiquity, Mediterranean pine nuts have been highly appreciated as gourmet food. They are used in the traditional Mediterranean and Middle Eastern cuisine, combined with meat, fish, salads, and vegetable dishes. Mediterranean stone pine nuts are a main component of Italian pesto sauce. Pine nuts are also baked into bread and pastry or used in chocolates and desserts, such as baklava. Recently the use of the nuts has gained new attention because, like other nuts, they are regarded as health food. Wild-collected pine nuts are among the most expensive nuts in the world, as a result of high harvest costs and the limited supply.

Stone pine cones and kernels moved along the trade routes of the ancient Mediterranean cultures since Neolithic times. They assumed cultural, symbolic and spiritual attributes. Stone pine became a holy tree devoted to the great mother goddess Cybele, and as such it played a major role in the spring equinox festivity (Hilaria) that celebrated the resurrection of Cybele's human lover Attis in the form of a pine tree (Kislev 1988; Gil 1999; Gil 2008). Extensive reviews of the cultural history of Mediterranean stone pine have been published (Romero 1886; Kislev 1988; Agrimi and Ciancio 1993; Prada et al. 1997; FAO 1998a; Gil1999;Martinezetal.2004;Gil2008).

B. Natural and Planted Area

Around the Mediterranean Sea, there are currently about 0.7 million hectares of stone pine-dominated forests, sparsely scattered from the Atlantic coast in Portugal to the shores of the Black Sea and Mount Lebanon (Fig. 4.1). Main distribution areas are in Spain (470,000ha), Portugal (80,000 ha), Turkey (50,000 ha), and Italy (40,000 ha). More than one-halfofthisareaistheresultofprotectiveafforestation(Martinez et al. 2004).

At the present time, the natural area and its range expansion as protohistoric archeophyte remain unknown (Rikli 1943; Feinbrun 1959; Thirgood 1981; Gil 1999) and is an issue that has not been solved by



Main distribution of Mediterranean stone pine forests.

m⁺, -./0genetics(Fallouretal.1997;Vendraminetal.2008).Thedistributio
nofstonepineprobablyarosefrommultiplelocationsin the northern
Mediterranean, with a presence in upper Tertiary sup- ported by fossil
evidence in the Iberian Peninsula and even in Austria (Men endez-
Amor1951;Klaus1989).InsouthernFranceandinSpain, stone pine has
been an integral element of the open woodland and steppe habitat
dynamics of the late Quaternary before and during the Last Glacial
Maximum (50–18 kyr BP), when pine nuts were gathered as easy-to-
store, highly nutritive (50% fats, 35% proteins) staple food by
Neanderthals and modern humans (Bazile-Robert 1981; Gil 1999; Badal
2001; Finlayson et al. 2006; Carrion et al. 2008, 2009). Its high
relevance or symbolism for the ancient hunting and gathering inhabi-
tants of southern Europe can be deduced from representations of the
tree’s umbrella-shaped crown and its kernels in Neolithic rupestral
drawings in the La Sarga Cave at Alcoy (Alicante, Spain) dated between
10,000and6,500yearsago(Hern andezP erezetal.2007).Inpalynolog- ical
studies and archaeological sites from Holocene, stone pine was found
throughout its current area, ranging from Portugal to Turkey and
Lebanon (Feinbrun 1959; Thirgood 1981; Ramil and Aira 1994; Franco-
Mú ‘gicaetal.2005;Garc ía-Amorenaetal.2007;RoviraandChabal2008;
Henry et al. 2010; Rubiales et al. 2010). Stone pine cones appear among
funeral offerings in ancient Egypt during the 12 dynasty (Schwein-
furth 1884), probably imported from Mount Lebanon along with cedar-
wood widely used in Egypt. During the Roman Empire, local cultivation was
extended for ornamental and symbolic use as far as the British Islands,
and it is still grown in Scotland as an ornamental. During the last four
centuries, European colonists have brought stone pine to other regions
with Mediterranean climates, such as Australia, Argentina, Chile,
California, and South Africa, where it became naturalized and in some
cases even considered an invasive species (Richardson and Higgins
1998).

C. Pine Nuts as Forest Products

1. Stone Pine Forests and Woodlands. Extensive research and devel-
opment has been conducted about the ecology and silviculture of
Mediterranean stone pine forests and, in particular, about its cones as
a nonwood forest product (cf. Castellani 1989; Agrimi and Ciancio 1993;
Calama 2004; Montero et al. 2004a; Calama and Montero 2007; Calama
et al. 2008; Montero et al. 2008; Ovando et al. 2010). Mediterranean stone
pine forests can be pure or mixed with other Mediterranean pines
(*P. pinaster* or *P. halepensis*), oaks (*Quercus ilex*, *Q. suber*, or *Q. faginea*),

o123567819:Juniperus communis, J. oxycedrus, J. thurifera, or J. phoenicea) without understory or accompanied by coppices of those oaks and by other Mediterranean trees and shrubs. Usually, pure stands are managed forests with a regular structure derived from sowing, plantation, or natural regeneration after clear-cutting or shelterwood cuttings. The stone pine forms a dominant stratum of even-aged trees, either with a nearly closed canopy layer, reaching final densities of 200–250 trees/ha at 100 years (if managed for timber production), or sparser to optimize the crown development, thus favoring cone production. In the later scheme, thinning is conducted early and intensively applied to attain a final density of 75–125 trees/ha at stand ages of 50–60 years (Montero et al. 2008). Most likely, in absence of management the natural stone pine stand structure would tend to be uneven aged and to form open woodlands with a canopy cover below 40% or even 20%. Saplings would be clustered into small even-aged groups growing under the influence of the crown shadow of elder trees. Enrichment with other species would be facilitated by pine-mediated soil evolution. However, in the genuine stone pine habitats in sandy flatlands and dunes, water rather than light is the main factor limiting growth. Thus, the competition is between roots, not between crowns, and the surface occupied by the root system of a tree exceeds 10- to 50-fold its crown projection, explaining the low canopy closure (Montero et al. 2004b). Stone pine forms part of Mediterranean ecosystems not only as a dominant species of the psammophilous azonal vegetation in coastal or inland dunes but also often as an accompanying species in mixed Mediterranean woodlands dominated by holm or cork oak or in shrublands where the crowns of stone pines spread sparsely over a main dominant layer of oaks, juniper, or bushes (Fig. 4.2). It occupies a similar ecological niche as *P. sabiniana*, also a dyszoochorous, self-fertile pine in the similarly open, fire-prone blue-oak woodlands in the Mediterranean climate of the Californian foothills (Ledig 1999).

2. Cone Production. In stone pine-dominated forests, cones are now the most important product, providing a higher income to the forest owners than timber and other products (Ovando et al. 2010). Nevertheless, this forest production is limited by site quality and subordinated to the ecological and social functions of these forests, mainly soil and watershed protection, biodiversity, and scenic beauty and recreational use.

Mean cone production varies widely both in time and in space. In stone pine, there is a large variation among years related to masting, the biological phenomenon of regional synchronized variation between annual yields as a result of endogenous or exogenous factors, mainly



Portugal (over 1,000 kg/ha in the Setubal district south of Lisbon where a temperate, humid climate allows for optimal and stable growth) (Castellani 1989; Oliveira 1995; Coelho 1997; Sabra and Walter 2001; Nanos et al. 2003; Gordo 2004; Calama and Montero 2007; Calama et al. 2008). Pine and kernel size can vary widely between sites, regions, and years, but the relative kernel output (per cone weight) is a quite stable ratio: 1,000 kg cones contain about 160 to 200 kg unshelled pine nuts and 40 kg shelled kernels (Gordo et al. 1999; Montero et al. 2004b; Calama et al. 2007b; Morales 2009). Another fact to take into account is that in natural stone pine forests, many trees (30%–80% in any year) do not bear any cones and nearly 10% of the pines never produce cones. Factors such as early stand ages, high stocking densities, soils with low water-hold capacity, and dry conditions increase the proportion of trees with null crops (Calama et al. 2010).

Until recently, the commercial cone harvest was carried out by men climbing the trees in late fall and winter to throw down the ripe but still-closed cones, with iron-hooked, 3–6-m-long poles (Fig. 4.3), each pine climber collecting about 300–450 kg cones per day (Gordo et al. 1999). In the last decade, cone gathering has been increasingly accomplished by harvesting machines that vibrate trees, similar to tree shakers used in olive harvests (Fig. 4.4), overcoming the shortage of skilled labor for the dangerous climbing on the often frozen or rain-wet pines during winter (Martinez-Zurimendi et al. 2009). Cones collected from the ground are transported and stored in depositories until summer. Then, the cones open naturally by exposure to the sun, and kernels are extracted similarly to the processing of other nut species (Trueb 1999; Batlle 2006).

3. Pine Nut Markets. The annual global Mediterranean stone pine nut production is irregular because of masting patterns that can affect several countries at the same time but varies around 30,000 tonnes (t) in shell; 6,000–15,000 t in Portugal (mainly from the Setubal district), 6,000–10,000 t in Spain (60% from western Andalusia, 30% Castile, and 10% Catalonia); and 1,500–5,000 t in Italy and Turkey (Castaño et al. 2004; Barranco and Ortúño 2004). However, production data are often unreliable for various reasons (Barranco and Ortúño 2004), particularly because of the traditional way harvesting is accomplished. Most harvesting is under contract with a forest owner paid a previously agreed price per hectare based on estimated yield. In some regions, pine nuts are collected mainly for local consumption, the cones being considered in some places a free commodity. In addition, there is significant cone pillaging. As a result, forest owners often do not know actual yields.



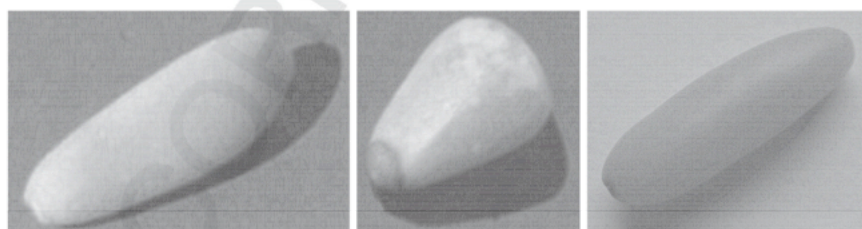


retail price of about US\$50–\$70 per kg. There is a limited supply of wild-collected pine nuts of this and other species with edible kernels. Although there are some substitutes, such as almonds, that could ease the demand, the price is quite inelastic, whereas the market is very elastic in terms of quantity, absorbing as much pine nuts as available (Trueb 1999; Sabra and Walter 2001; Barranco and Ortuño 2004; Sharashkin and Gold 2004; Batlle 2006; Fuentes 2009; Jurado 2009).

More than 20 pine species produce large, edible seeds that are (or were) used as staple food by local populations, although pine nuts of only a few species are traded at international markets (FAO 1998b). These species

include three Asiatic ones: *Pinus koraiensis*, *P. gerardiana*, and *P. sibirica*. China alone makes up for about 80% of international pine nut exports, mainly from *P. koraiensis* (Fig. 4.5), traded at a current price about US\$10 per kg. Other species include American pinyons, *Pinus edulis*, *P. monophylla*, and especially *P. cembroides* (“piñón rojo”), none of which produces kernels as tasty and rich in protein as the genuine Mediterranean pine nuts from *Pinus pinea* (Trueb 1999; Batlle 2006). In Mediterranean stone pine nuts, the most abundant fatty acids are unsaturated (85%), mainly linoleic acid (45%–48%) and oleic acid (36%–40%). Pine nuts are also rich in essential minerals, such as magnesium (3,600–4,300 mg/kg), phosphorus (970 mg/kg), potassium (7,500–8,800 mg/kg), iron (70–130 mg/kg), and copper (27–39 mg/kg) (Loewe et al. 1997; Montero et al. 2004a). Dietary values (Table 4.1) differ greatly with pine species (Destailats et al. 2010).

The world crop of pine nuts is not sufficient to satisfy the increasing demand. Over the past decade, countries such as China and Pakistan became the main exporting countries of pine nuts gathered from different



4.1. Dietary value of some shelled pine nuts.

Subgenus	Species	Protein(%)	Fat(%)	Carbohydrate (%)
Pinus	<i>P.pinea</i>	33–38	46–51	5–6
	<i>P.sabiniana</i>	28–30	54–60	9
Strobilus	<i>P.cembra</i>	17–18	50–59	17
	<i>P.sibirica</i>	17–19	51–75	12
	<i>P.koraiensis</i>	17–18	65–67	12
	<i>P.strobiformis</i>	28	52	7
Ducampopinus	<i>P.cembroides</i>	19	60–65	14
	<i>P.edulis</i>	14	61–71	18
	<i>P.monophylla</i>	10	23	54
	<i>P.cuadrifolia</i>	11	37	44
	<i>P.maximartinezii</i>	31	43	2
	<i>P.gerardiana</i>	12–14	51–61	20–23

Source: Lanner 1991; López-Mata 2001; Montero et al. 2004a.

The botanical origin of imported pine nuts is not reported on labels and therefore are difficult to trace by consumers in spite of the disparate range of prices and qualities. Over the last years, an emerging phenomenon of taste disturbances after consumption of Chinese pine nuts has been reported, putatively caused by seeds of *Pinus koraiensis*, *P. armandii*, or even *P. massoniana*, the latter not being listed as a common source of edible pine nuts by the FAO (1998b). The symptoms are an unpleasant bitter, metallic taste that appears 1–3 days after consumption and lasts for days or weeks, sometimes combined with food aversion (Mostin 2001; Destailats et al. 2010; Moeller 2010; Munk 2010). Although very unpleasant, these symptoms, known as pine mouth or pine nut syndrome, are self-limited and resolve without treatment. The causes are still under discussion but might be related with rancidity after excessive exposure to light, air, or heat during inadequate processing, storage, and packaging. Also, irritating terpenoid compounds are found naturally in *Pinus massoniana*; the high content of pinolenic, taxoleic, or other polyunsaturated fatty acids in Asiatic pine nuts, but not in *P. pinea*, might stimulate the enteroendocrine system to enhance bile production and release. An induced excessive bile secretion was pointed to as possible direct cause of the metallic, bitter taste after consuming pine nuts (Moeller 2010).

The forests of Korean and Siberian stone pine are threatened by heavy logging pressure and destructive cone harvesting techniques that endanger future sustainability (Sharashkin and Gold 2004). In addition, over-harvesting of virtually the complete seed yield for human consumption

thenaturalregenerationoftheAsianchilgozapine,thesameasinseveralr
areAmericanpinyonsrestrictedtoafewlocalpopulations (Ledig et al. 1999;
Ledig et al. 2001). In contrast, during the last century, the
Mediterranean stone pine has experienced a range expansion as well as
a large increase in planted area in its native countries. In the future,
farmland afforestations could yield more pine nuts than the natural
forests, although there is uncertainty because of climate change effects
on the edge of temperate and xeric climate zones in the Mediterranean
area (Mutke et al. 2006).

II. BOTANY

A. Taxonomy and Genetics

~~Pinus pinaster~~ Pinus is the largest and most important genus of conifers
with more than 100 species, spreading mainly on the northern
hemisphere. Pine forests are highly relevant forest types in boreal and
temperate climate zones, for both economic and ecological reasons.
Because of their commercial importance, several pine species are grown
in plantation forestry for timber and pulpwood, often out of their natural
range (Mirov 1967; Farjon 2005).

Within the subgenus Pinus (hard pines), the section *Pinea* includes
besides Pinus pinea the other true Mediterranean pines (*P. pinaster*, *P.*
halepensis, *P. brutia*, *P. eldarica*, and *P. canariensis*) and some related
Asian species. Within this group, the stone pine does not hybridize and
differs greatly from its congeners in its ecology and reproductive
strategy in the fire-prone Mediterranean ecosystems. Its large, wingless
seeds are dispersed by animals, while the other Mediterranean pines
have small, long-winged, wind-dispersed seeds. They are also adapted
to recurrent wildfire. Many provenances of maritime pine (*P. pinaster*)
and Aleppo pine (*P. halepensis*) show fire-mediated serotiny, with
Canary Island pine (*P. canariensis*) being even a sprouter, two properties
absent in *P. pinea* (Mirov 1967; Klaus 1989; Tapias et al. 2004).

2. Other Pines with Edible Kernels. There are numerous species with
large, animal-dispersed seeds throughout the genus Pinus.

Subgenus *Ducampopinus*. These include the species cluster of Amer-
ican pinyon pines, comprising the subsection *Cembroides*, especially
P. cembroides, *P. edulis* *P. monophylla* and five minor species restricted
to small areas—*P. orizabensis*, *P. johannis*, *P. discolor*, *P. culminicola*, and

¡Ç£¤¥¦§¨ª«¬®¯°±²³´µ¶·¸¹º»¼½¾¿(syn.*P. juarezensis*)—thesubsectionRzedowskianae (*P. rzedowskii*, *P. pinceana*, *P. maximartinezii*), and the subsection Nelsonianae (*P. nelsonii*). The pinyons were named by the Spaniards when they found pines with nutlike seeds in Mexico, taking the original Spanish name from *P. pinea*, pino piñonero (pine-nut pine). There are two Asiatic species, *P. gerardiana* and *P. bungeana*, in the subsection Gerardianae.

Subgenus *Strobus*. This includes the group of five-needle stone pines (subsection *Cembrae*) *P. cembra*, *P. sibirica*, *P. koraiensis*, *P. pumila*, and *P. albicaulis*, as well as the Chinese *P. armandii* and the American *P. strobiformis*, both subsection *Strobi*.

Subgenus *Pinus*. Only a few species are found, namely the big-cone pines (subsection *Ponderosae*) *P. sabiniana*, *P. torreyana*, and *P. coulterii*, and the sole species in subsection *Pineae*, our *P. pinea* (Sauer 1988; Lanner 1981, 1998).

This list shows that the ecological-evolutionary trait of large seeds as adaptation to dyszoochory (dispersal by seed predators) is quite frequent in the genus and has arisen independently several times in different phylogenetic lines, although it is unique in stone pine among the Mediterranean pines. Nut-producing pines exhibit a wide variety of life history and ecological characteristics. Many of them are adapted to marginal habitats in stressful, xeric, or tree line conditions, where they fulfill important ecological functions, such as soil and watershed protection, wildlife food, nesting, and roosting facilities that give them an ecosystem-wide relevance (Tomback and Linhart 1990).

3. Genetic Variation in Mediterranean Stone Pine. Although stone pine has disjunct populations widespread throughout its Mediterranean range, the species seems to lack not only any population or phylogeographic structure but virtually any neutral genetic variation within or among its populations. Its extremely low level of diversity at chloroplast and nuclear markers is truly exceptional among abundant, widespread trees and is attributed to a severe and prolonged demographic bottleneck long before its quaternary dispersal over its current distribution range (Fallour et al. 1997; Vendramin et al. 2008). However, new molecular marker data point to two differentiated gene pools at the westernmost and easternmost edges of the Mediterranean Basin and a more complex demographic scenario (G.G. Vendramin, pers. commun.). The few studies published to date regarding variation in quantitative traits coincide in reporting only minor or nonsignificant differences between populations,

There were clear phenotypic differences between clones or families studied in grafted orchards or in vitro (Court-Picon et al. 2004; Gordo et al. 2007; Cuesta et al. 2008; Mutke et al. 2010). Nevertheless, perhaps as a consequence of the genetic depletion, some very characteristic, common traits in stone pine were shared by all studied trees. One of these was a pronounced sensitivity to compact soils that hampers the early growth and development in stone pine, resulting the tree height variation in its plantation array a perfect bioindicator of microsite variation with spatial autocorrelation, similarly to genetically homogeneous hybrid poplar plantations (Mutke et al. 2007b, 2010).

Some of the most genetically depauperate pine species are large-seeded dyszoochorous pines such as *P. torreyana* or *P. maximartinezii*, with very restricted distribution ranges, as well as, to a lesser extent, *P. sabiniana* and *P. coulteri* (Ledig and Conkle 1983; Mattes 1994b; Ledig et al. 1999; Grotkopp et al. 2002; Johnson et al. 2003). Apart from historical processes, such as population bottlenecks or founder effects after long-distance dispersal by birds (Ledig 2000; Cuenca et al. 2003), there might be some putative advantages of evolving self-compatibility (a factor that accounts for the low genetic variability in these pines) related to a frequent clustering of kin trees derived from seed caches that might produce endogamy among sibling within the same “founder” cluster. An example would be the kin tolerance to tissue fusion by root grafting, observed also in Mediterranean stone pine, or kin selection resulting in crowding tolerance (Tomback and Linhart 1990; Bruederle et al. 1998; Schoettle and Rochelle 2000).

Against this background, the low genetic variability in stone pine, while not unusual per se, is significant in relation to its wide, disjunct geographic range along the Mediterranean (Vendramin et al. 2008). The most plausible explanation remains occasional long-distance dispersal by anthropic seed transfer, perhaps as easy-to-store trail food of migrating hominids since the Paleolithic, as also suggested for European hazel during early Holocene (Kuester 1998), or by modern human transfer since the Neolithic cultures throughout the area. As already underlined for the dispersal of American nut-bearing pines along Indian routes, the durability of hard-shelled pine nuts and their easy epigenous germination are qualities that allow new local founder populations to establish even from a few dropped seeds (Lanner 1981; Ledig 1999).

The life-history traits isolate *P. pinea* from its most direct relatives within the group of Mediterranean pines. The very reduced genetic diversity might indicate that it is a mere relict taxon from former Tethyan flora. *Pinus pinea* is clearly an emblematic key species of the current

~ 0.230

landscape, similarly to *Pinus canariensis*, a relict species that was widely distributed in the Tertiary but is restricted now to the Canary Islands, where its forests are nevertheless a characteristic and abundant forest type (Frankis 1999).

B. Morphology

1. General Description. Stone pine is an evergreen, resinous tree that can exceed 20 m in height at 40 to 60 years, reaching 35 m in some monumental trees with stem diameters up to 2 m (Fig. 4.6) (Earle 2009). Nevertheless, in its natural resource-limited habitat, height growth is quite slower, dominant trees being more likely to be about 10–20 m or even less when culminating, with diameters of 30–50 cm at the end of the silvicultural rotation (80–120 years). The adult needles are 10–20 cm long, flexible, and growing in fascicles (dwarf shoots) grouping 2 (occasionally 3) needles with a persistent basal scale sheath. New needles appear only on elongating new shoots and persist 2–3 years. Hence, there are 2–3 needle cohorts on the extremes of each branch, though needles can persist some years under favorable conditions, such

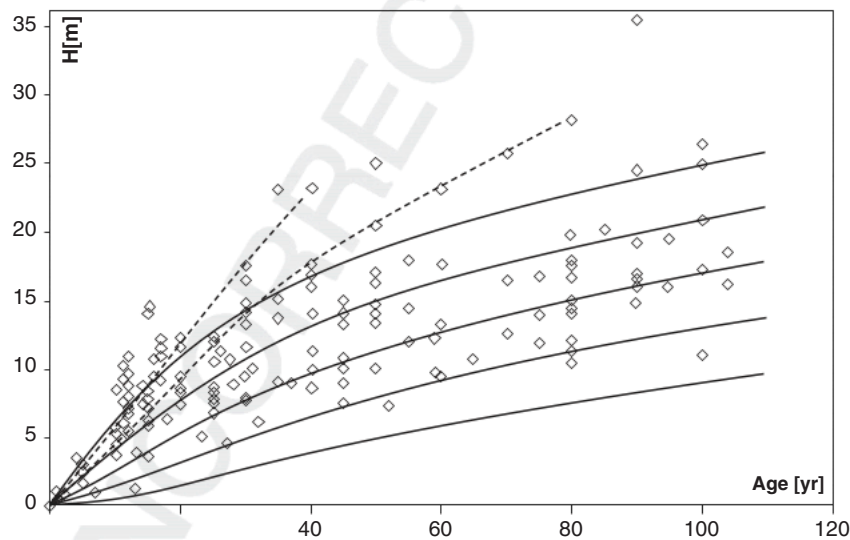


Fig. 4.6. Growth curves for even-aged stone pine stands in Spain (continuous lines; Calama et al. 2003) and 165 tree heights throughout central Chile (open diamonds, dashed lines; Loewe et al. 1997; V. Loewe, pers. commun.).



sending vertical tertiary roots that explore deeper ground layers. The genetic homogeneity of stone pine facilitates that neighbor trees are tolerant to fuse their roots by spontaneous graftage (anastomosis). Sometimes even living stumps can be observed remain alive due to neighboring trees, although they are unable to sprout their own adventitious shoots (Montero et al. 2004b). Pines are obligate symbionts with mycorrhizal fungi and benefit from the mycelium's higher absorptive capacity for water and mineral nutrients. Stone pine associates with species of the genera *Rhizopogon*, *Suillus*, or *Pisolithus*, among others. The most interesting mycorrhizal partner is the saffron milk cup, *Lactarius deliciosus*, a highly priced edible mushroom that can be inoculated on *Pinus pinea* in nursery plants, making its gathering in pine plantations an attractive complementary income (Loewe et al. 1997).

2. Tree Architecture. Stone pine is a gymnosperm. Although in harsh environments, gymnosperms can dominate the landscape or whole biomes, in many other ecosystems, they must be considered evolutionary relicts. They are old life-forms that evolved in the Mesozoic and are more primitive than modern dicots. They are characterized frequently with a fixed crown architectural model, are wind-pollinated, and most shed wind-dispersed seeds from normally ligneous cones. The crown architecture of pines is based on a regular branching pattern forming whorls at the apical end of the annual shoot and follows Rauh's model defined by Halle and Oldeman (1970). This tree architecture model is determined by a monopodial orthotropic trunk that grows rhythmically, developing whorls of branches. The main branches are morphogenetically identical with the trunk, and the reproductive structures are lateral without effect on the topology of the shoot system.

Like most pines from temperate climates, stone pine is normally uninodal; each apex elongates its terminal bud in a single flush in spring (April–June) into an annual shoot that forms on its tip a new whorl of lateral branch buds (and female cones) and the new terminal bud. This implies that the growth is predetermined the year before within buds that are set at the end of spring, resting for nearly one year. In dominant shoots of young and vigorous stone pines, however, the bud can skip dormancy and start elongating immediately after its formation, completing in early summer a second (and rarely even a third) shoot and whorl, known as *Lammas* growth. This second shoot is always quite a bit shorter than the first, exceeding rarely 10cm. The phenology of shoot elongation in spring depends on the air temperature and can be predicted by accumulated degree day sums (Lanner 1976; Klaus 1989; Mutke et al. 2003).

One characteristic feature of stone pine is the singular candelabra-like, polyarchic crown architecture. Its umbrella shape is determined developmentally from the initiation of each branch layer, due to an apical dominance of the leader shoot minor than in most other conifers that show a clear hierarchic growth habit. In these species, a conical crown shape results with an orthotropic trunk and tiers of less vigorous, inclined or horizontal branches. In contrast, in open-grown stone pines, the lateral branches are also orthotropic and grow during several years as much as if not more in diameter and length (and branching rate) as the stem. This pattern gives rise to a crown wider than deep, spherical in youth and characteristically wide, smoothly rounded to nearly flat in older trees, and umbrella-like once the basal branches are lost or pruned (Ruiz de la Torre 1979; Lanner 1989; Mutke et al. 2005c).

The crown architecture of stone pine has a high phenotypic plasticity in response to light. The exogenous effect of self-shading on branch vigor substitutes to some degree for the missing endogenous axis hierarchy of apical dominance. There is a positive feedback of secondary growth and axis position, because together with the leader shoot, only those codominant branches whose tips remain in the upper canopy in full light can stiffen by secondary (i.e., diameter) growth and consequently suffer less downward-bending than other shaded, less vigorous branches that undergo a steep loss of apical growth and branching. Thus, position advantages lead to higher photosynthetic rates and growth and vice versa. In lateral shaded trees—at forest edges, for example—the growth of each branch responds to its individual light yield, resulting in a strong canopy asymmetry. This phenotypic plasticity in response to light is a strategic trade-off, favoring in a closed canopy (competition for light) the height growth forming a narrow single-stem crown and limiting female cone formation to the leader shoot. Once the crown reaches full light conditions, its growth switches to the open polyarchic shape that enhances seed production by maximizing the number of codominant, cone-bearing shoots on the broad expanding crown surface (Mutke et al. 2005c).

The low growth rate and poor stem form of *P. pinea* is determined by the lack of apical dominance. In the absence of regular pruning, Mediterranean stone pine does not produce marketable saw timber but timber usable only for processing to chip- or fiberboard.

3. Reproductive Structures. Pines are monoecious and anemophilous, bearing male (staminate) and female (ovulate) strobili in spring on current-year shoots, although in different axes. In stone pine, female strobili are borne only at the tip of vigorous, orthotropic shoots. In an architectural analysis of stone pine trees, female strobili were found only

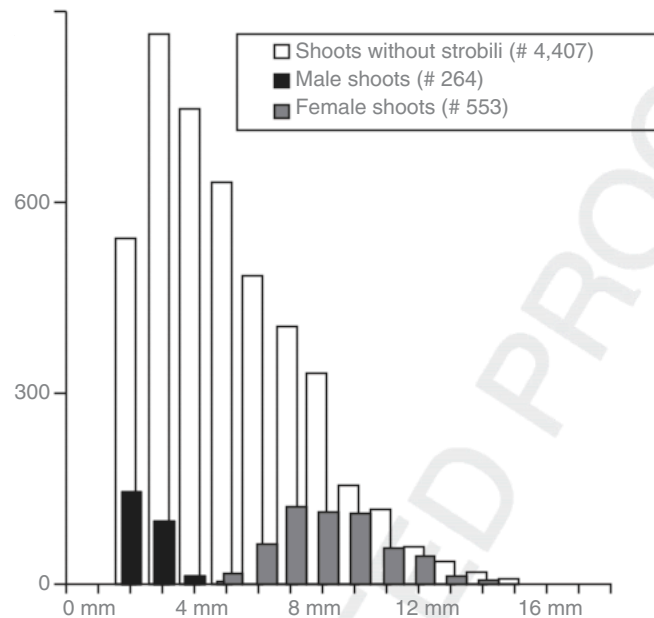


Fig.4.8. Diameter distribution of sprig shoots in Pinus pinea with or without male or female conelets (Mutke 2005c).

general shoot diameter distribution of 2–16 mm (Fig. 4.8), although even in the most vigorous shoots, their probability was less than 40% (Mutke et al. 2005c). The male strobili, on the contrary, are produced on the slender shoots of lateral or dominated branchlets (diameters 2–5 mm, the lower end of the general shoot diameter distribution), many of which are in the lower crown. There are many small, yellowish pollen cones compactly grouped at the base of each shoot, occupying often more proportion of its length than the needle fascicles.

The female strobili are yellow green, isolated or sometimes 2 or more together at a shoot apex. Each female strobilus has a separate peduncle with scarios bracts, which serve to envelop it before it expands; its form is oval, and its length about 1 cm. After wind pollination in spring, the scales of the strobilus augment in thickness and become firmly pressed against each other before lignification. During the first year, the cone grows minimally; in the second year, it becomes globular (about the size of a walnut). It does not reach its final size (8–15 cm long, 5–10 cm wide) until the summer of the third year, when fecundation and embryogenesis

h taken place, although the seeds within do not ripen until the end of autumn (Francini 1958).

The whole process from pollination to cone opening takes 3 years, one more than in most other pines, and the ripening cones are found a whorl deeper in the crown, below the last year's needle cohort. With an average number of 3 branches per whorl, this additional year means a 5-fold increase in needle biomass (and photosynthetic gain) on or above the cone-bearing shoot for the sustainment of the cone, in addition to a better mechanical support of the heavy cones on a thicker shoot. In contrast, other wind-dispersing pine species that ripen their cones in 2 years often produce them on lateral branches, scattering the small, long-winged seeds when the ripe, open cones are moved by the wind, the same as the airborne pine pollen released by the male strobili on slender lateral shoots.

4. Ontogenetic Heteroblasty. Another feature of the genus *Pinus* that must be taken into account in orchard management of stone pine is heteroblasty—that is, the presence of two different shoot (and needle) types along the axes that mark the juvenile and the vegetative adult phase of the tree. After germination, the juvenile stone pine seedlings bear isolated, short (<2cm) bluish-green juvenile needles and have a slow, not-preformed growth and a diffuse branching pattern, if any at all. They lack a terminal winter bud but cease growing in autumn with a simple needle rosette at the apex. After the vegetative phase change, the adult needles (10–20 cm) appear in fascicles of 2, and a true terminal bud is formed at the end of spring (Lanner 1976). In stone pine, the vegetative phase change does not occur at a fixed age but depends on reaching a certain threshold size. This implies another singular ecological trait of this species: the phenotypic plasticity in its ontogeny, or its ability to delay this phase change in limiting environments, such as in xeric sites or with excessive competition in a closed understory, for years or even several decades in order to survive until this threshold size is met and the growth pattern can switch to the adult phase (Fig. 4.9).

In stone pine, the juvenile phase in normal site conditions will last 3–5 years and delays the onset of vigorous height growth and crown development. This may be seen as a necessary ecological-evolutionary trade-off for improving seedling survival in the marginal habitats occupied by this species in the unpredictable Mediterranean climate where annual rainfall can vary widely (200–800mm). Several cohorts of juvenile seedlings can subsist nearly in standby, waiting for the next humid couple of years to undergo the phase change simultaneously and starting stem elongation.



c loss (e.g., by wildfire). In stone pine, adventitious juvenile-like shoots derive only from reactivating the dormant apical meristems of the dwarf shoots that bear the needle pairs. This short-term response rebuilds photosynthetic tissues after needle loss, but these will be topped and relegated to the inner crown by the growth of other adult shoots in the following years. Only in cases of severe dieback of whole crown sectors may those shoots prosper and close the gap, although several years will pass before the adult growth habit recovers and reconstitutes new structural branches. Since green needle fascicles with dormant buds last only 2–3 years, and these are produced only on the extremes of each branch, older and basal growth units can not resprout once the foliage is shed. In consequence, the possibility of redirecting crown development by pruning (e.g., for horticultural purposes) is quite limited; branches can be eliminated, but no routine crown renovation can be achieved by adventitious responses to pruning as in dicot orchard trees.

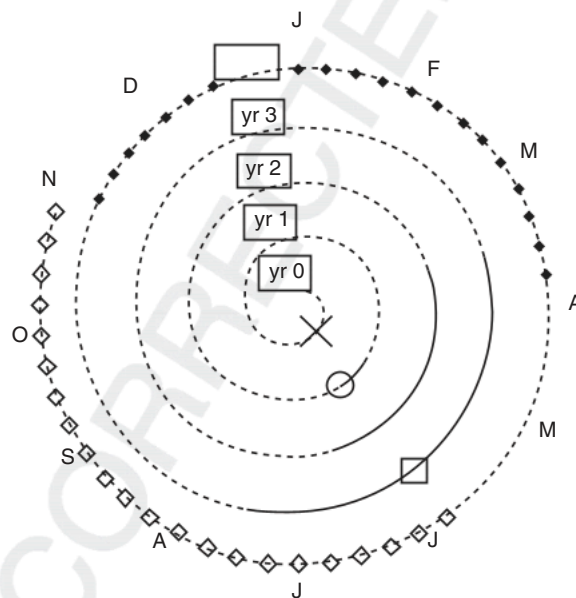
C. Reproductive Biology

Reproductive Maturity. Stone pine saplings normally undergo the reproductive phase change to sexual maturity several years after the vegetative phase change. Although in vigorous leader shoots the first conelets can appear as early as age 5–8 years, the reproductive effort will be limited for years. During this time, most of the lateral buds in each whorl are vegetative, resulting in four to eight branches per whorl; in reproductively mature trees, a whorl normally bears 2–4 branches and the rest of the lateral bud primordia convert to female conelets (Mutke et al. 2005c). At age 10–15 years, male maturity is reached, and in open-grown saplings, the presence of female cones with normally developed seeds is common at 15–20 years of age (Tapias et al. 2001). The vegetative adult but reproductively immature phase accounts for the most vigorous height and diameter growth of the tree, with higher branching rate and absence of reproductive costs.

2. Reproductive Development. Conelet primordia are preformed inside the shoot bud one year before emergence and pollination. The female strobili appear during the spring flush of the bud when the shoot reaches about one-half its final length. Raised on the highest shoot apices, the strobili point into the air like little lightning conductors fishing for electrostatically charged airborne pollen grains, being receptive when shoot elongation nearly finishes but before the new needles close in the shoot apex. Although male and female conelets appear at different times on the developing shoots, blooming is synchronous; hence, no

! "#\$%&'!impedimentforautopollinationexists.Pollinationis several weeks later than in sympatric *P. pinaster* and *P. halepensis*, in early April in coastal southern Spain and at the end of May or even in June in colder inner or northern provenances in Spain or in Italy. Blooming dates can vary several weeks between years, depending on the accumulated heat units; each 1 °C increment of air temperature brings blooming forward about one week. The cone and seed develop slowly during two years; in the third spring, the pollen tube is formed, fecundation takes place, and the seed ripens until autumn (Fig. 4.10) (Francini 1958; Abellanas and Pardos 1989; Mutke et al. 2003). The coincidence of three cone cohorts in the tree was mentioned by Pliny the Elder in *Historia Naturalis* (Liber XVI,

Chap. XLIV): "in maxima tamen admiratione pinus est: habet fructum maturescentem, habet proximo anno ad maturitatem venturum ac deinde tertio" (the pine, however, is the most remarkable of them all; for it has upon it at the same moment the fruit that is hastening to maturity, the



(*)+4.10. Reproductive development of stone pine cones, lasting nearly 4 years from primordia formation in the bud (cross, year 0), conelet pollination (open circle, year 1), ovule fecundation (open square, year 3) until seed shedding (open diamonds) if cones are not harvested the winter before (closed diamonds). Periods of cone growth are marked by continuous lines. Spring phenology is referred to colder inland regions; in warmer coastal zones, it is about 2 months earlier (Abellanas and Pardos 1989; Mutke et al. 2003).

f, -./ that is to come to maturity in the ensuing year, and the fruit that is to ripen the next year but one). It implies that a singular critical event, such as extreme frosts or summer droughts, might place several consecutive yields at risk (Mutke et al. 2000b).

Ripe cones are heavy, broad-ovoid, 8–15 cm in length, weighing 250–350 g, sometimes up to 500 g. Each cone contains about 80–120 large, nearly wingless seeds, 2 per cone scale. These pine nuts are 1–2 cm in length, weighing about 0.6 g, pale brown with a powdery coating that is cinnamon brown in autumn and black when the seeds are ripen for harvesting. If not predated by squirrels or gathered by humans in autumn or winter, the cones will open in the spring of the fourth year, and the seeds will be spread or predated during summer and fall (Mutke et al. 2003).

3. Seed Dispersal in Natural Habitats. In stone pine, the vestigial seed wing is ineffective for wind dispersal, and the seeds are preyed and accidentally dispersed by rodents or birds. This strategy of being secondarily dispersed by seed predators (dyszoochory) is shared with other large-seeded pines and probably evolved independently in different phylogenetical lineages, despite being an expensive strategy for organisms compared with the dispersal of small, long-winged seeds by wind, habitual of most pine species (Foster 1986; Tomback and Linhart 1990). The nutmeat of the stone pine is nutrient and energy rich with 50% lipids and a high protein content of 30%–35%. The packed aggregation of many seeds in large cones that need three years to ripen makes them susceptible to complete loss by various abiotic or biotic risks. As a defense, the stone pine allocates 96% of the cone mass to woody structures (cone scales and thick seed coats) to protect the kernels, possibly as a coevolutionary response to predispersal seed predation by the European red squirrel or as fire adaptation (cf. Johnson et al. 2003; Siepielski and Benkman 2007, 2008). Unlike the pinyon and 5-needle pines of subgenera *Ducamopinus* or *Strobus*, no specific symbiotic Corvidae are known as main seed disperser of *P. pinea* (nor for any of the large-seeded species in subgenus *Pinus*), putatively because the presence of squirrels would have constrained their coevolution (Tomback and Linhart 1990; Johnson et al. 2003; Molinari et al. 2006; Siepielski and Benkman 2007, 2008). Thus optimization of seed dispersal cannot rely on adjustments of a species-specific symbiosis, as described for the other subgenera (Vander Wall and Balda 1977; Mattes 1994a; Tomback 1994; Vander Wall 2002), but apparently only on an unspecific, mere maximization of seed output in mast years, not only to attract generalists—mainly blue-winged magpie (*Cyanopica cyanus*), European magpie (*Pica pica*),

0122345 crow (*Corvus corone*), and ground-foraging rodents such as the wood mouse (*Apodemus sylvaticus*)—but also to achieve the so-called predator swamping that allows some seeds to escape predation (e.g., in not-retrieved scatter hoards) (Herrera et al. 1998; Obeso 2002).

The relative success of this seed dispersal strategy would have led Mediterranean stone pine, by positive feedback selection, to a special reproductive investment. Thus, the biomass allocation to cones is similar to stem growth, which in many sites is less than 1 m³ per hectare per year (Cabanettes and Rapp 1981; Montero et al. 2004b). This represents a reproductive effort unique among European pines or other forest trees whose biomass allocation to reproductive structures is normally equivalent to less than 10% of stem growth (Helmisaari et al. 2002). The umbrella-shaped, polyarchic crown architecture of Mediterranean stone pine must then be interpreted as a way to enhance maximal seed production by increasing the number of codominant branches capable of sustaining and nursing the heavy cones (Lanner 1989; Mutke et al. 2005c). Similar broad, multibranched canopies with upward-oriented branches characterize other large-seeded pines (Tomback and Linnart 1990). The smooth, contoured upper surface of the stone pine presents a mass of orthotropic cone-bearing branches that are both visible and accessible to flying birds (Lanner 1989).

D. Ecology

Several thorough reviews about the ecology of Mediterranean stone pine characterize its central and marginal habitats in the wild (Romero 1886; Agrimi and Ciancio 1993; Gandullo and Sanchez Palomares 1994; Blanco et al. 1997; Prada et al. 1997; Montero et al. 2004b; Montero et al. 2008). Nevertheless, there are few studies about agronomic boundaries and optimal ranges of the autecological parameters for this tree species, due to its lack of cultivars and large-scale production out of forests. There are examples of other narrow endemic pine species with restricted current range far from their autecological optimum, such as *P. torreyana*. Torrey pine is in its natural coastal, drought-prone habitat a wind-battered, open-crowned tree only 5–15 m high, but it produces straight trees up to 45 m high in plantation forestry in Australia or New Zealand. Another example is the emblematic *P. radiata*, with 15–30 m in its natural range but up to 65 m in New Zealand. The dominant height of natural *P. pinea* stands reaches 25 m at 150 years at the best sites (Calama et al. 2003), but in Chile, some trees have reached this height at 40–50 years, 28 m at 80 years, and seem to be still increasing (Fig. 4.6).

Stone pine grows in its natural Mediterranean range at low or montane altitudes (up to 1,000 m; 1,500 m in Lebanon), although planted stands can be found at 2,000 m, as in Chile. Stone pine is considered thermophilous and xerophilous. The mean annual rainfall in its population ranges from about 400 to 800 mm or higher (1500 mm), with 15 to 125 mm in summer (4-month summer drought), although often with a very irregular distribution among season and years. Growth and reproductive processes are dependent on the yearly or seasonal rainfall. In years with less than 350–400 mm rainfall or after dry springs, shoot elongation, secondary growth, needle length, needle longevity, cone and kernel size, and strobilus induction are reduced, particularly in excessively drained, deep sandy or shallow rocky sites with reduced water-holding capacity. Beyond 600 mm, further annual rainfall increases do not seem to improve these parameters (Mutke 2005; Mutke et al. 2003, 2005a, 2005c,c). The mean annual temperature in its natural range is 10–18 °C; the average temperature in the warmest and coldest month is 21–26 °C and 3–11 °C, respectively, with extreme temperatures above 40 °C and occasionally below 20 °C in dry continental inland

provenances, stone pine generally does not suffer any frost damage, and the late blooming date avoids injury in the reproductive organs, but extreme frosts can damage or even abort developing cones in the first and second year (Mutke et al. 2003). In areas with humid maritime influence, the frost tolerance of foliage and shoots is lower (Agrimi and Ciancio 1993). The open crown structure does not tolerate heavy wet snowfall; thus, the altitudinal and latitudinal limits of the habitat of the species is marked by snowfall recurrence rather than by temperature.

2. Soil. The stone pine can pioneer poor habitats such as mobile dunes or limestone because of its robust root system. Most natural stone pine woodlands grow on incipient soil types, such as arenosols, regosols, and lithosols, or mature cambisols or luvisols on better sites. The species is quite tolerant to pH ranging from moderately acid to basic (pH 5–9), although neutral soils are preferred. Active limestone is frequently 0% in siliceous soils, but at up to 16%, no negative effect on growth is observed in Spanish provenances. There are spontaneous stone pine forests on calcareous soils with active limestone about 35%–40% and even in presence of gypsum, although the site quality for the species decreases in those soil conditions (Gordo 2004; Calama et al. 2008). Some afforestation on calcareous soil in Israel shows chlorosis and reduced growth (G. Schiller, pers. commun.).

Soil structure is important for stone pine, because roots prefer well-aired soils with loose textures, such as sand, sandy loam, or gravel (with water-holding capacity of at least 60 mm). In compact clay or silt soils

EGHIJ less than 40% sand and more than 40% silt or more than 30% clay), root development is restricted, especially in the first phase of seedling establishment, and can delay flowering for many years, fixing the plant ontogeny in a stationary juvenile state. Therefore, a thorough soil preparation with deep plow is required before planting to achieve early production. However, stone pine can survive and prosper in heavy soils as long as they are not waterlogged and there is no excessive interspecific competition (Agrimian and Ciancio 1993; Gandullo and Sánchez Palomares 1994).

III. HORTICULTURE

In Cultivated Plantations. In the cultural history of stone pine, most current stands are natural or naturalized forests or protective afforestations, the latter especially from the last 150 years; cultivated plantations for pine nut production are still rare. Market prices for pine nuts and the crisis of traditional rain-fed crops in Mediterranean countries have drawn attention to stone pine as an alternative woody crop on farmland. Stone pine has been widely used in farmland afforestation after the European Common Agricultural Policy reform in 1992 with set-aside payments, combining public subsidies with the expectation of future cone production. The tolerance of this pine to poor soils, dry climates, and late frosts and its resistance to diseases and pests have increased private initiatives to promote intensively managed stone pine plantations for pine nut yield in several Mediterranean countries, especially in Portugal, where the benign climate favors high cone yields (Mutke et al. 2000a; ANSUB 2006; Ovando et al. 2010).

Most plantations for pine nut production are still managed as extensive forestry or agroforestry systems, and trees are mostly grown from seeds. Only in southeastern Spain are there references to traditional local use of stone pine grafted on Aleppo pine stocks (Cavanilles, 1797; Sánchez, 1902). As in other fruit and nut tree crops, grafting offers several important advantages. In Italy, Portugal, and Spain, research on clonal selection and grafting techniques has been undertaken with stone pine to transform it to a horticultural crop (Baudin 1967a; Balmat 1971, 1974; Magini and Giannini 1971; Gilet al. 1987; Gil and Abellanas 1989; Catalán 1990, 1998; Abellanas et al. 1997b; Prada et al. 1997; Mutke et al. 2000b; Castañero et al. 2004; Gordo 2004; Mutke et al. 2007a).

The prime advantage of grafting is that it allows the propagation of selected superior genotypes. Grafting mature scions also skips the rapid

gKLMNO juvenile stage and reduces the delay in production from 20 to less than 10 years. Grafted trees develop their adult, open-branched, cone-bearing “upper” crown from the beginning and allocate a high proportion of resources to cone formation; hence their height can be one-half that of even-aged seedling trees. The resulting short stem greatly reduces manual harvest costs because cones can be knocked off the tree with long poles from the ground or from ladders, without having to climb the trees. In the future, mechanized harvesting from grafted orchards might utilize milder tree shakers than those used for wild pines.

2. Mean Cone Yields in Grafted Plantations. There are very few published yield studies of grafted stone pine plantations. Those that exist are mainly from forestry plantations on nonagricultural land transformed by in situ grafting, often without scion identity and normally without any cultural treatments once established. Furthermore complete records of annual yields are not always available (Fig. 4.11). Average annual yield does not reach 1,000kg cones/ha in the first 10 years after grafting (80–160kg unshelled seeds, 20–40kg shelled seed). However, grafted plantations on farmland with crop management are expected to have higher yields. At present, there are no data on the performance of grafted stone pines older than 15–20 years. However, the oldest grafts are nearly

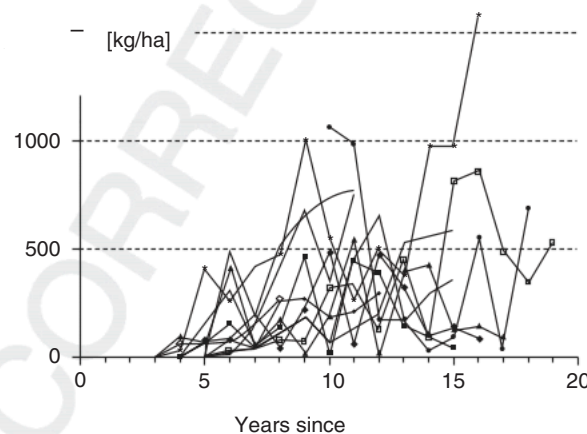


Fig. 4.11. Cone yield series in grafted stone pine plantations or clone trials. Bold line: a wide-spaced orchard on a riverside with a high groundwater level and regular weed control by harrowing, thus the water availability reduces yield variability (Data from Castaño et al. 2004; Catalán and Catalán 1996; Magini and Giannini 1971; Mutke et al. 2005a, 2007b; and unpublished data).

senescence.

A. Clone Selection

Since the early 1990s, several grafted clonal trials have been established in Spain and Portugal within the framework of regional and national research programs for the characterization of the crop and the tested genotypes. The results of these trials underscore the relevance of genetic and environmental factors for seed-yield quantity and quality. The collections contain ramets of several hundred candidate clones derived from selections in several geographical regions based on outstanding cone yield in the forest (Abellanas et al. 1997a; Iglesias 1997; Gordo 1998, 2004; Castañeda et al. 2004; Mutke et al. 2005a, 2007b).

In several analyzed trials, the degree of genetic determination for average annual cone yield (kg/tree) was estimated at 0.15–0.40, resulting in a similar expected genetic gain (12%–39%) selecting the top 10% of the tested genotypes. Since the genetic correlations between genetic values for cone yield and mean cone or seed size were always positive ($r = 0.17$ – 0.47), no trade-off between crop quantity and quality was observed (Mutke et al. 2005a, 2007b). Within the legal regulation of the European Union about Genetic Forest Resources (Council Directive 1999/105/EC, 22 December 1999, on the marketing of forest reproductive material, OJEC of 15 January 2000, L 11/17–40), the commercial release of the best clones depends on their previous, still-pending inclusion in the National Register of Basic Materials, that will allow the marketing of scions or grafted young trees in the categories “qualified” or “tested” as defined by the Directive. Further research on quantitative genetics of stone pine, such as progenies trials or controlled crosses, will allow increased knowledge and breeding gains. New multisite clonal trials have been established, because in the few existing replicated clonal trials, clear clone $\times$ site interactions were observed, with different clones being the most productive in each agroclimatic zone (Mutke et al. 2007b).

The greatest proportion of individual yield variation in the analyzed trials was associated with the disparate tree size. Although about 15% of tree size variation itself depended on the genotype, in 70% it was associated with microsite variation (spatial autocorrelations), underlining the common steep reaction norm of stone pine to soil properties. Thus, the genetic improvement of the species has to be complemented with adequate soil preparation and management practices that optimize tree growth and vigor (Mutke et al. 2005a, 2007b, 2010).

1. Seedlings. Stone pine seeds can germinate after many years when stored dry and cold. No other pregermination treatment of the seeds is required other than a 48-hr soak in water to soften the shell and separate empty or rotten seeds that float. In order to obtain nursery-raised plantlets with a good root ball (e.g., as rootstocks), planting containers are recommended, preferably with root pruning systems that avoid root circling. For direct planting of nongrafted trees, seedlings should be planted out during the first autumn (e.g., from 0.250L containers) or moved to larger containers each year to avoid root strangling. The earlier the plant is installed in the field, the better its definitive root system will develop. The same applies for cultivating rootstocks in the nursery.

2. Grafting. In stone pine, rooting of cuttings and woody grafting are unsuccessful. The most often used vegetative propagation technique is tip-cleft grafting, substituting in spring the 5–15-cm-long terminal bud of the stock's leader shoot with a bud scion of the selected clone, always joining nonwoody tissues. Scions are obtained from long shoot buds (still-green soft tissue) in spring, at the moment of spring flush initiation and always before the needle tips arise from the sheath. In order to guarantee fast callus production and early sap supply between tissues, it is best if the stock is slightly more advanced, facilitated by being produced in the greenhouse, after bud burst, but always before complete shoot elongation. Consequently, phenology constricts the window of time for grafting to about 2 weeks each spring: in March in the warmer southern area, in May in the Spanish inner highlands. There can be variations of several weeks between years, depending on the accumulated degree day sum (Mutke et al. 2003).

When inserting the scion in the cleft of the cut leader shoot of the rootstock, no plant growth regulators or sealing paste is needed, but the graft is tied with parafilm or polyethylene ribbon and protected for several weeks by a transparent, perforated plastic bag. During grafting, lateral stock branches are cut back to avoid competition with the scion; they are completely removed in autumn once the graft's own needle biomass is sufficient to nurse the whole tree (Gil et al. 1987; Castaño et al. 2004).

Stone pines seedling used for rootstocks are about 2–5 years old, after reaching the vegetative adult phase with a terminal bud that can be substituted by the scion. Aleppo pine rootstocks have been used for calcareous soils in thermo-Mediterranean climate zones; at least during the first 15–20 years, no incompatibility has been observed (Catalan

1998; Catalán and Catalán, 1996). Although there are no direct experimental comparisons between stone pine and Aleppo pine rootstocks in these soil conditions, we have observed that ungrafted stone pines close to orchards grafted on Aleppo pine perform well and do not show any edaphic misadaptation that would exclude the use of stone pine as rootstock. In sandy soils, stone pine grafted on Aleppo pine perform worse than on stone pine rootstocks, developing sparser crowns and weaker, less blooming shoots. Thus, further experiences are necessary before recommendations of different stock types can be made.

The first extensive grafted plantations in the 1970s were conducted in the field, using 2–5-year-old stone pine rootstocks. In southern Spain, several hundred hectares of afforestations recently have been transformed by *in situ* grafting. But in harsher site conditions, grafting success in the field can drop drastically because of inclement weather. Instead, 2–3-year-old rootstocks grown in 1–3-L containers are used for grafting in greenhouse and autumn outplanting. In coastal Andalusia with temperate winters, occasional autumnal grafting in the field has been successful; the graft union forms in winter because in this climate, the physiological activity of the tree is not shut down completely in winter, as in inland regions.

Another feasible technique is needle grafting. A small portion of the shoot, or scutcheon, that bears a single needle fascicle (dwarf shoot) is inserted in a similarly shaped hole made on the rootstock (Palomar et al. 1993). However, the resulting scion shoot and crown is less vigorous and performs worse than long-shoot bud grafting.

In vitro micropropagation techniques, such as micrografting, rooting of microcuttings, induced organogenesis, and somatic embryogenesis, have been carried out without conclusive results in the field, because of the difficulty of acclimatizing the laboratory plants to Mediterranean outdoor conditions (Cortizo et al. 2004; Alonso et al. 2006).

C. Site Selection

Stone pine orchards might compete economically as an alternative to traditional crops, especially in rain-fed, marginal farmland, in climatic regions analogous to the stone pine's natural range or more temperate and humid climates, though avoiding zones with risks of heavy snowfalls. Stone pine prefers loose sandy soils with root access to groundwater, but not waterlogged, as in sand layers over river terraces. It also produces well on stony sites (*terra rossa* or *terra fusca*) or gravels, but too compact clay or silt interferes with the root development. These preferences should be taken into account to avoid a delay in production.

cones formed on the orchard trees will be insufficient to provide ideal pollination and cone setting during the first 10 or 15 years, even if nongrafted “pollinator” seedlings are planted between the grafts. Consequently, to avoiding this delay in yield initiation, some mature stone pines for anemophilous pollen supply should be available nearby.

D. Planting

Site Preparation. Depending on the soil type and the previous land use, deep-plowing (60 cm) with a ripper or mole plow is highly recommended before planting to favor a sound root development and vigorous crown growth.

2. Tree Spacing. Because of the phenotypic plasticity of crown development that depends on light, tree spacing within the orchards must be wide enough to avoid lateral shading that would limit codominant, orthotropic shoots. In addition, excessive competition limits water availability, the main limiting factor in Mediterranean climates. Dense plantings (3 × 3 m, 1,111 trees/ha) of grafted clone collections show delayed production and a strong yield variability among years (Fig. 4.11). Annual mean cone yields were normally less than 2 kg/tree during the first decade, especially in trials where canopy cover was completed in a few years and trees could not develop the expanding-crown ideotype. In contrast, with increased spacing (6 × 6 m, 278 trees per hectare), the best trees reached mean annual cone yields of 4–6 kg (1,100 kg/ha) and maximum yields of 12–15 kg (3,000–4,000 kg/ha) in less than 10 years after grafting. Both the initial delay and the existing yield variation between years (masting) reflect (apart from the harsh environment in inner Spain, where these plantations are located) the nearly complete lack of pruning, fertilization, or weed and pest control in most of these plantations, since they were established primarily as gene banks rather than agronomic trials. Spacing of 6 × 6 m or wider seems advisable, depending on site conditions. This distance allows for tractor passage for tilling and mechanical harvest by tree shaking.

The response of pine cone yield to different spacing has been studied in two thinning experiments (Mutke et al. 2007a). The first one was a pine grove grafted in situ 5 years after plantation was established (850 trees/ha), using mass-selected, nonlabeled scions. Twelve years after grafting, canopy closure was excessive, and a systematic thinning was applied by removing two-thirds of the grafted trees. The response of the remaining trees (285 trees/ha) was immediate with strobili induction for the following year. Since then, the trees in the thinned plots have grown more, reaching a mean basal area (BA; i.e., the sum of stem sections above the

times that the unthinned control plots (BA point) of 8.5 m²/ha seven years later, yielding each tree a crop of 417 m²/ha). Thus, the canopy opening reequilibrated the crown growth and nearly doubled the annual mean cone yield per hectare from 170 to 320 kg in the last 7 years, although the dependence on rainfall, which varied from only 172 to 416 mm among years, was responsible for a strong variation as a result of the low water holding capacity of the gravel soil in the plot (Mutke et al. 2007a).

In another orchard, a clonal trial planted at 3 m with trees grafted the year before in nursery, the crowns closed in a few years, and the BA was nearly 12 m²/ha before a thinning was applied 12 years later, combining four different treatments: (1) thinning by removing half of the trees, (2) light pruning by thinning out only lower or inner weak and shaded branches, (3) a short seasonal weekly irrigation of 50 L/tree during June and July during the period when cone growth finishes, and (4) untreated control plot. The trees in the thinned replicates (pruned or not) rendered consistently four times the cone yield of the unthinned and nonpruned control (i.e., two times per hectare (707 vs. 350 kg/ha and year; BA 12 vs. 15 m²/ha 5 years after thinning), even more in the irrigated replicate (848 kg/ha and year) during the 4 years it was irrigated (Fig. 4.12). The pruned but unthinned replicate rendered 50%

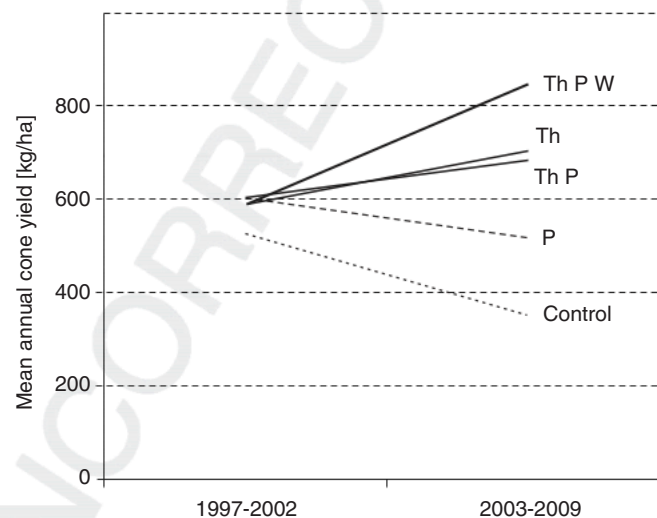


Fig. 4.12. Mean cone yield before and after treatments that combined thinning (Th ½ 550 trees per ha), pruning (P ¼ weak thinning out in lower and inner crown) and/or watering during 4 years (W ¼ 200–400 L per tree per year during June–July).

than the control (516kg/ha and year). The mean cone weight, a variable related directly to the mean size of the extracted pine nuts, increased about 40% after thinning (282 vs. 200 g), whereas no significant effect of pruning or watering on cone or seed size was found.

These very preliminary experiments indicate that BA, at least in those drought-prone environments, should not exceed 10m²/ha to avoid excessive competition. Thus, an initial spacing of 6 m is sufficient until the tree mean diameter surpasses 20cm. Then an alternate thinning in quincunx spacing can reduce the density to half, 138trees/ha at 8.5m between diagonal tree lines, which would be adequate until a mean diameter about 30cm. Water is the main limiting factor in the study sites. This can be demonstrated from irrigated stone pine specimens in parks or golf courses that show a consistently higher cone yield and reduced masting (yield variation among years).

E. Cultural Practices

The management of grafted stone pine is similar to other fruit tree orchards, although specific cultural techniques must be adapted for this conifer crop (Batlle 2006).

1. Soil Management. As in any rain-fed woody crop, effective weed control by tilling is important. This can be accomplished superficially with a disk harrow in order not to damage the subsuperficial pine root system, or with a plow, if it has been done regularly since planting to favor deep root systems. Weed control by herbicide spraying has not been attempted.

Yield increments in cone number and size have been achieved by application of fertilizers, especially with dolomite (magnesium) on oligotrophic sands or gravels. Amelioration by addition of organic matter would improve soil structure and water and nutrient retention capacity. However, the optimization and profitability of these interventions is still under study (Castaño et al. 2004; Calama et al. 2007a). Special care must be taken with raw animal manure that might damage the sensitive conifer roots or mycorrhiza. Moreover, nutrient uptake will depend mainly on the water availability, which is the principal shortage in the stone pine's growing area.

Irrigation improves tree vigor and cone yield. However, even if there is access to a water supply, stone pine irrigation is unlikely to be a profitable investment alternative compared with other irrigated crops (Castaño et al. 2004; Mutke et al. 2007b).

Since stone pine female flowering occurs only on the most vigorous annual shoot tips on the crown surface and there is no adventitious sprouting from the wood of eliminated branches, virtually no pruning is applied in the upper crown. Pruning of the shade crown has not shown to influence greatly the upper shoots, except in excessively dense plantations, where tree thinning should be applied instead. Although some weak or lower branches might be eliminated to facilitate cultural or harvest operations, pruning as a cultural treatment does not appear to be economically feasible.

If there is no external pollen supply from nearby adult stone pine stands, pollination will depend on male flowering of the orchard. Thus, the weak dominated branchlets of the lower shaded crown will be essential to support a correct cone setting. It appears that the development of vertically differentiated crowns with enough pollen output might be the main limiting factor for early production of new orchards established out of existing stone pine growing areas. This shortcoming can be solved by an artificial, electrostatic pollen supply, used routinely in other conifer seed orchards (Pinillos and Cuevas 2008), but it is a short-term solution to force young plantations into early production and can hardly be justified economically. A better alternative is to optimize the growth conditions for achieving a fast, but equilibrated crown development of the trees for an early induction of both female and male strobili.

3. Pest and Disease Control. Few pests or diseases affect vigorously growing pines. The larvae of the pine processionary moth, *Thaumetopoea pityocampa*, can cause some defoliation, although stone pine is more resistant to this pest than other sympatric pines. The moth population is easily controlled by chemical treatments, as it is one of the most common pests on pines whose control is habitually from the air at greater scales. In plantations of small, grafted trees, it can be eradicated mechanically by removing its winter nests from the crowns, if an organic-agriculture label forbids pesticide use.

Rhyacionia buoliana and *R. duplana* are pine shoot moths whose larvae can damage or destroy the developing buds in spring by burrowing, impeding the normal shoot growth and female flowering that would have been initiated on the shoot tips. The moth can damage many shoots, especially in young or stressed plantations, but can be controlled chemically in late spring and by pheromone trapping.

The cone-boring larvae of two insects, the weevil *Pissodes validirostris* and the moth *Dioryctria mendacella*, can destroy or diminish yield significantly if populations are not controlled. But the moth larvae

©³«-® inside the cones during cone harvest in winter; hence damaged cones, once collected, can be sorted out easily by their different, brownish color, and destroyed. The control of the rarer and less spreading weevil requires a timed chemical treatment during its short imago phase inspring(Baud in1967b).

The western conifer seed bug, *Leptoglossus occidentalis*, is a recently arrived cone pest from North America that is considered an invasive species in Europe, where it is expanding its range. The stings of the nymphae damage cone development and can abort the seeds, causing considerable harm in the commercial cone yield in some regions (Vazquez et al. 2009). Another virulent, invasive pine pest spreading recently in Europe is the pine wilt nematode *Bursaphelenchus xylophilus*, although stone pine seems to be resistant, even in mixed stands in Portugal where *Pinus pinaster* trees are affected and killed by the nematode.

F. Harvesting

Cone harvest takes place in late autumn and winter (November–March). The small grafted trees do not usually exceed 5–6 m in height over several decades, allowing harvesting from the ground without necessitating the high costs of skilled pine climbers. In future commercial grafted plantations, cones might be gathered by harvesting machines, a technological change that began only in this decade in traditional pine forests. The first tree shakers were special machines, heavily armored against the falling cones; cheaper solutions exist today, such as special vibrating jaws coupled onto front-end booms of farm tractors or even on compact utility tractors with armored cabins (Fig. 4.4). When mechanical harvesting is envisaged, the lower tiers of the tree branches should be pruned in order to form a robust, straight cylindrical stem of at least 2 m beneath the crown base to allow the free shaking and swinging of the vibrated crown. Clean basal stems and a bare-soil management will guarantee the orchard's defense from spreading occasional fires that are a recurrent element in Mediterranean forest and farmlands. Strips with a few spaced tree lines of grafted stone pines have been tried out successfully as fire defense areas along roadsides or forest tracks, self-financing the bare-soil maintenance with the incomes from the cone yield (Prada et al. 1997).

G. Postharvest Processing

After cones are harvested, traditionally they are stored until summer and then laid out in the sun for opening, although there is a tendency to open the cones earlier in the year in stoves because of market requirements.

When the cones are opened, the cones are ground through a mill and the pine nuts are separated by sieves and cyclones from cone scales and fragments. The pine nuts in shell can be stored for years without becoming rancid. Before mechanical shelling, the seed shell is soaked in water for a greater elasticity that avoids kernel fractures; once shelled, the kernels are sieved and cyclone separated from the husk. Further processing consists of humidity standardization; polishing with sawdust; and classification by size, wholeness, and color, using for the latter electronic colorimeters and a posterior manual control; finishing with sterilization and packing, quite similar to industrial processes for other nuts (Trueb 1999; Barranco and Ortúño, 2004; Castaño et al. 2004; Batlle 2006; Jurado 2009). Since 95% of the processed material consists of husk, shell, and cone fragments, with low humidity (12%), low fly-ash content (2%), and high specific surface area, this subproduct is valued as biomass, sold for use in specific stoves (for seed shells) or transformed into pellets, reaching US\$0.05–\$0.08 per kg in local markets.

IV. CONCLUDING REMARKS

The characteristics and particularities of *Pinus pinea* set this gymnosperm apart from classic fruit or nut tree crops and explain why this species, used by ancient cultures of the Mediterranean, has only recently been taken from wild-harvested to a domesticated cultivated crop. The high prices obtained for this nut in international markets have made it an attractive opportunity as an alternative crop on rain-fed farmland or in agroforestry systems. Furthermore, its good performance on poor or eroded soils and positive response on better sites, few pests or diseases, reduced need for cultural practices such as pruning, and high resistance to climate adversities such as drought and extreme or late frosts make it a good candidate for conversion to a horticultural crop in contrast to its present use as a gathered crop in natural forests. Advances in propagation, harvest, and processing make this a promising new crop for Mediterranean climates.

The current knowledge about stone pine as a nut crop in specific plantations is still limited. The genetic control of seed productivity seems to be largely quantitative; no related major genes are yet known, and genomic approaches for their discovery are lacking. The association of vegetative and reproductive vigor in the same shoots limits any potential selection of highly productive dwarf cultivars for a modern intensive horticultural system. Managed grafted trials with selected genotypes indicate that productivity of forest land can be increased

3' μ' ¶ · 10» ¼ in comparison with yields in traditional stone pine forests. The major potential for stone pine as a crop appears to be both in agroforestry systems that combine isolated pines or tree lines, such as shelterbelts with farmland or pastures, and proper orchard plantations, especially on marginal stony or sandy Mediterranean farmlands where herbaceous crops or grazing are no longer profitable and where traditional afforestation would offer only environmental benefits but no direct income for the land owner. In southern Europe, this agronomic limit currently is being pushed forward toward better soils by the European common agricultural policies and by ongoing rural depopulation. With this background, the profitability of stone pine orchards and the standardization of the processing and finished product might extend its use as a crop in Mediterranean climate zones around the world.

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