

Biology and impact of Pacific Island invasive species. #11. *Cinchona pubescens* (red quinine tree) (Rubiaceae)

By Heinke Jäger*

Abstract

Cinchona pubescens Vahl (red quinine) is an evergreen tree ranging in height from 10–25 m with broad leaves and white or pink fragrant flowers arranged in clusters. Growing at altitudes between 130 and 3,300 m, it is one of 23 species in the genus *Cinchona* and has a natural distribution from Costa Rica to Bolivia. *Cinchona pubescens* has been cultivated in tropical regions, e.g. in South America, Africa, China, India and Indonesia, for its quinine-containing bark and has become invasive in some regions. This is especially the case in the Pacific region where *C. pubescens* has invaded the humid highland areas of Galápagos, Hawai'i, and Tahiti. It shades out and reduces the cover of native plant species and adversely affects endemic birds. In addition, it changes the microclimate and nutrient cycling in the soil, especially phosphorus, in Galápagos. The characteristics which make it such a successful invader include the production of numerous, windborne seeds and vigorous vegetative reproduction by re-sprouting from underground stems and fallen trees. In Galápagos, *C. pubescens* is currently being manually controlled by uprooting the trees and by applying herbicides to cuts in the bark. However, this method requires continuous hand pulling of seedlings to be successful. Disturbance by control actions appears to facilitate the establishment and invasion by other non-native plant species, especially blackberry (*Rubus niveus*). Quinine and other alkaloids extracted from *Cinchona* bark are still being used for medicinal purposes today and the wood is increasingly used as construction material in Galápagos. Ironically, *C. pubescens* is now considered rare and endangered in its native range in Ecuador.

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Cinchona pubescens Vahl (red quinine) is an evergreen tree ranging in height from 10–25 m with broad leaves and white or pink fragrant flowers arranged in clusters. Growing at altitudes between 130 and 3,300 m, it is one of 23 species in the genus *Cinchona* and has a natural distribution from Costa Rica to Bolivia. *Cinchona pubescens* has been cultivated in tropical regions, e.g. in South America, Africa, China, India and Indonesia, for its quinine-containing bark and has become invasive in some regions. This is especially the case in the Pacific region where *C. pubescens* has invaded the humid highland areas of Galápagos, Hawai'i, and Tahiti. It shades out and reduces the cover of native plant species and adversely affects endemic birds. In addition, it changes the microclimate and nutrient cycling in the soil, especially phosphorus, in Galápagos. The characteristics which make it such a successful invader include the production of numerous, windborne seeds and vigorous vegetative reproduction by re-sprouting from underground stems and fallen trees. In Galápagos, *C. pubescens* is currently being manually controlled by uprooting the trees and by applying herbicides to cuts in the bark. However, this method requires continuous hand pulling of seedlings to be successful. Disturbance by control actions appears to facilitate the establishment and invasion by other non-native plant species, especially blackberry (*Rubus niveus*). Quinine and other alkaloids extracted from *Cinchona* bark are still being used for medicinal purposes today and the wood is increasingly used as construction material in Galápagos. Ironically, *C. pubescens* is now considered rare and endangered in its native range in Ecuador.

[Insert Figure 1]

Cinchona L. is likely the most commercially important genus of the family Rubiaceae after the genus *Coffea* L. due to its quinine-containing bark. *Cinchona pubescens* Vahl (syn. *C. succirubra* Pav. ex Klotzsch, 1857, red quinine tree) has been introduced worldwide, mainly

from Bolivia, Colombia, Ecuador, and Peru (Andersson 1998), and is considered among the 100 of the worst invaders globally (ISSG 2013). It is highly invasive on several Pacific island groups, especially Galápagos, Hawai'i, and the Society Islands (Weber 2003), where it forms dense stands in the humid highland vegetation, reducing plant species diversity and abundance. The invaded islands are Santa Cruz in Galápagos (Jäger et al. 2009), the island of Hawai'i, Maui and O'ahu in Hawai'i (Starr et al. 2003), and Tahiti in the Society Islands (Vanquin 2006). The introduction of the novel "tree" life-form to a formerly treeless environment in Galápagos led to significant changes in vegetation stand structure and changes in light, water, and nutrient regimes (Jäger et al. 2007, 2009, 2013, Figures 2 and 3). Consequently, *C. pubescens* is now considered an ecosystem engineer in Galápagos (Jones et al 1994, Jäger et al. 2009). In Hawai'i, *C. pubescens* has invaded native understory and forest canopy vegetation, as well as nonnative forests and disturbed areas, where it reduces the cover of other plant species (Starr et al. 2003, Fischer et al. 2009, Figure 4). In Tahiti, *C. pubescens* has invaded secondary and primary rainforests and undisturbed cloud forest (Meyer 2004, Vanquin 2006, Figure 4).

This review synthesizes information on the ecology, impact and management of *C. pubescens* world-wide, which is partly published in grey literature and therefore not easily accessible.

[Insert Figures 2-4]

NAME

Cinchona pubescens Vahl

Phylum Angiospermae, class Magnoliopsida, order Gentianales, family Rubiaceae, tribe Cinchoneae, genus *Cinchona* L.

Synonyms: *C. asperifolia* Wedd., *C. caloptera* Miq., *C. chomeliana* Wedd., *C. colorata* Laubert ex B. D. Jacks., *C. cordifolia* Mutis, *C. cordifolia* var. *macrocarpa* Wedd. ex Howard, *C. cordifolia* var. *microcarpa* Howard, *C. cordifolia* var. *peruviana* Howard, *C. cordifolia* var. *rotundifolia* (Pav. ex Lamb.) Wedd., *C. cordifolia* var. *vera* Wedd., *C. coronulata* Miq., *C. decurrentifolia* Pav. in Howard, *C. delondriana* Wedd., *C. discolor* Hayne, *C. elliptica* Wedd., *C. erythroderma* Wedd., *C. goudotiana* Klotzsch ex Triana, *C. govana* Miq., *C. grandifolia* Ruiz & Pav., *C. hirsuta* Ruiz & Pav., *C. lechleriana* Schtdl., *C. howardiana* Kuntze, *C. lutea* Pav. in Howard, *C. microphylla* Mutis ex Lamb., *C. morada* Ruiz, *C. obovata* Pav. ex Howard, *C. ovata* Ruiz & Pav., *C. ovata* var. *erythroderma* Wedd., *C. ovata* var. *rufinervis* Wedd., *C. ovata* var. *vulgaris* Wedd., *C. palescens* Vell., *C. pallescens* Vitman, *C. pallescens* var. *ovata* (Ruiz & Pav.) Howard, *C. pelalba* Pav. ex DC., *C. pelletieriana* Wedd., *C. peruviana* Howard, *C. platyphylla* Wedd., *C. pubescens* var. *cordata* DC., *C. pubescens* var. *ovata* (Ruiz & Pav.) DC., *C. pubescens* var. *pelletieriana* Wedd., *C. pubescens* var. *purpurea* (Ruiz & Pav.) Wedd., *C. purpurascens* Wedd., *C. purpurea* Ruiz & Pav., *C. purpurea* Vell., *C. rosulenta* Howard ex Wedd., *C. rotundifolia* Pav. ex Lamb., *C. rubicunda* Tafalla ex Wedd., *C. rufinervis* Wedd., *C. rugosa* Pav. ex DC., *C. scrobiculata* Humb. & Bonpl., *C. scrobiculata* var. *delondriana* Wedd., *C. scrobiculata* var. *genuina* Wedd., *C. subcordata* Pav. ex Howard, *C. subsessilis* Miq., *C. succirubra* Pav. ex Klotzsch, *C. succirubra* var. *conglomerata* Howard, *C. succirubra* var. *cuchicara* Howard, *C. succirubra* var. *erythroderma* Howard, *C. succirubra* var. *spruceana* Howard, *C. succirubra* var. *vera* Howard, *C. tenuis* Ruiz ex DC., *C. tucujensis* H. Karst., *C. viridiflora* Pav. ex Howard, *Quinquina obovata* (Pav. ex Howard) Kuntze, *Q. ovata* (Ruiz & Pav.) Kuntze, *Q. pubescens* (Vahl) Kuntze, *Q. succirubra* (Pav. ex Klotzsch) Kuntze (Andersson 1998, Grandtner 2005, IPNI 2005).

Common names: English: red cinchona, red quinine tree, Peruvian bark, Jesuits' bark, Countess bark; Dutch: kinaboom; French: quinine, quinquina rouge; German: Chinarinde, Chinarindenbaum; Spanish: cascarilla, quina, quinina.

Cinchona pubescens can be easily confused with *C. antioquiae* L. Andersson, *C. barbacoensis* H. Karst, *C. capuli* L. Andersson, and *C. micrantha* Ruiz ex. Pav. (Andersson 1998). However, none of these are found in the Pacific islands.

The genus *Cinchona* was named after the Countess of Chinchón, wife of the Viceroy of Peru, by Linnaeus in 1742. A confusion over Spanish, Latin and Italian orthography resulted in the loss of the first "h" in the genus name and "*Cinchona*" became established (Keeble 1997). According to a well-cited legend, the countess was cured of malaria by having been administered the bark of *Cinchona* in 1638 after all other remedies failed (Hill 1952, Prendergast and Dolley 2001) and it was not until 1930 that this story was proven to be false (Keeble 1997).

Due to its medical importance, *Cinchona* has historically attracted a lot of attention from taxonomists. During the 19th century, many different names were established based on minor morphological differences (Popenoe 1949, Harling & Andersson 1994). The taxonomy of *C. pubescens* is especially complicated, since it frequently hybridizes with other *Cinchona* species (Acosta Solís 1945b, Camp 1949, Harling and Andersson 1994, Andersson 1998), especially with *C. barbacoensis* H. Karst., *C. calisaya* Wedd., *C. lancifolia* Mutis, *C. lucumifolia* Pav. ex Lindl., *C. macrocalyx* Pav. ex DC., *C. micrantha* Ruiz ex. Pav. and *C. officinalis* L. (Andersson 1998).

DESCRIPTION AND ACCOUNT OF VARIATION

Species Description

Cinchona pubescens is an evergreen tree, 10–25 m tall, with a diameter at breast height (DBH) of 20–80 cm in Ecuador (Acosta Solís 1945b, Andersson 1998) and 30 m tall with a DBH of 90 cm in northern Peru (Hodge 1948). In Ecuador, the trees usually have a main trunk that branches in the upper third forming a semicircular-shaped crown (Acosta Solís 1945b). In its introduced range in Galápagos and Tahiti, trees can reach a height of up to 15 m and a DBH of 10–30 cm (Shimizu 1997, Vanquin 2006, Jäger 2011). The maximum height of trees measured in the Makawao Forest Reserve on Maui, Hawai'i, was 16 m (Fischer 2007).

The leaves are opposite, broad and membranous, 8.3–23 cm long and 5.3–21 cm wide, ovate to suborbicular with pubescent petioles (1.2–5 cm long) and stipules that can be caducous (Andersson 1998, Figure 5). Leaf blades have 7–11 pairs of prominent secondary veins and are commonly hairy beneath, especially the young ones. Leaf domatia are usually absent but if present, they are pouch-shaped (Andersson 1998).

The inflorescence of *C. pubescens* is usually large, with broad panicles up to 20 cm, and sometimes longer (Figure 5). Flower corollas are pinkish or purplish, paler at base (corollas outside may be white to light pink or red in Hawai'i, Tahiti and Galápagos) and are fragrant (Andersson 1998, Starr et al. 2003, Meyer pers. comm. 2013, Figure 5). The corolla tube is 9–14 mm long, glabrous inside and pubescent outside. The seed capsules are ellipsoid to subcylindrical and 13–41 × 5–7 mm long, opening from the base to tip when mature (Figure 5). Seeds are 7–12 × 2.1–2.8 mm, light and have dentate wings (Andersson 1998, Figure 5).

[Insert Figure 5]

Distinguishing Features

A conspicuous feature of *C. pubescens* is that its senescing leaves turn yellow or bright red. *Cinchona pubescens* also possess unique growth characteristics in its Pacific island distribution. In Galápagos, it produces a main trunk but also often develops several trunks a short distance away, which emerge by suckering of underground stems (see Del Tredici 2001). This way, *C. pubescens* trees take on a multi-stemmed growth form, with the individual stems connected below the surface (Shimizu 1997, Figure 6). In addition, it re-sprouts from fallen and cut stems to produce vertical shoots (Macdonald et al. 1988). Contrary to its growth form in mainland Ecuador, trees produce branches on the lower third of the trunk, which are bent upwards, resulting in a semicircular to cylindrical crown in Galápagos (Figure 6). The same is true for trees in the Makawao Forest Reserve on Maui (L. Fischer pers. comm. 2014).

[Insert Figure 6]

Intra-specific Variation

The leaf morphology is variable, especially with respect to size, shape, and hairs of the leaf blades. Reasons for this variation could include local differentiation and clinal variation in response to altitude (von Humboldt 1808, Acosta Solís 1945b), as well as hybridization with other *Cinchona* species (Andersson 1998). To my knowledge, no work on the potential genetic variation within *C. pubescens* has been carried out. However, since the species is so wide spread and hybridizes with other species, it is an important topic for investigation.

Illustrations

As well as the figures provided in this review, a good cross-section of images are available on the following websites:

Photos from Hawai'i by Kim and Forest Starr:

<http://www.starrenvironmental.com/images/species/?q=cinchona+pubescens&o=plants>

Global Invasive Species Database:

<http://www.issg.org/database/species/ecology.asp?si=63&fr=1&sts=&lang=EN>

CABI Bioscience Invasive Species Compendium, Datasheet *Cinchona pubescens*

<http://www.cabi.org/isc/datasheet/13484>

ECONOMIC IMPORTANCE AND ENVIRONMENTAL IMPACT

Detrimental

Studies carried out on *C. pubescens* in different Pacific island ecosystems generally indicate detrimental impacts on the native vegetation. Common negative effects included the reduction of species abundance and diversity. In Hawai'i, *C. pubescens* out-competes other species in dense *Dicranopteris linearis* vegetation zones, as well as in mesic and wet forests, especially *Acacia koa* forests in the Makawao Forest Reserve on Maui (Starr et al. 2003, Figure 4). The herb and shrub cover in this reserve were also reduced in invaded areas (Fischer et al. 2009). In Tahiti, *C. pubescens* has invaded secondary and primary rainforests and undisturbed cloud forest (Meyer 2004, Vanquin 2006). It now dominates native forests in West Java (Junaedi and Mutaqien 2010). In the highlands of Santa Cruz Island in Galápagos, *C. pubescens* dominates the Fern-Sedge zone and co-dominates the Miconia zone, formed by the endemic shrub *Miconia robinsoniana* Cogn. In both vegetation zones, *C. pubescens* is reducing species diversity and is adversely affecting species cover, especially that of endemic IUCN Red List species, like *Justicia galapagana* Lindau and the tree fern *Cyathea weatherbyana* (C.V. Morton) C.V. Morton (Jäger et al. 2007, 2009), as well as *Scalesia pedunculata* Hook. f. in the Scalesia zone (Shimizu 1997). These effects were attributed to the introduction of a tree to formerly treeless vegetation zones of the Galápagos Islands, where *C. pubescens* is now considered an ecosystem engineer (Jones et al. 1994, Jäger et al. 2009). *Cinchona pubescens* affects the microclimate in areas where it has invaded by reducing the photosynthetic active radiation by 87 % and by increasing

precipitation as it intercepts the highland fog with its broad leaves, which also increases relative humidity (Jäger et al. 2009). The concentration of phosphorus in senesced *C. pubescens* leaves is double that of the concentration found in green leaves and consequently, the phosphorus concentration in the leaf litter and soil of *Cinchona*-invaded areas is significantly higher compared to non-invaded areas (Jäger et al. 2013). This, along with a high specific leaf area and a faster decomposition rate, suggests that *Cinchona* enhances phosphorus cycling in the soil (Jäger et al. 2013). This pattern was confirmed over a 2-year study (Jäger unpubl. data), indicating an increase in the soil phosphorus concentration over time. In other systems, enhanced phosphorus levels in soils may drive species losses (Wassen et al. 2005) but whether or not this has a negative impact on the native Galápagos flora, which is adapted to phosphorus-poor soils, is currently unknown. It is likely though that increased phosphorus concentrations in the soils facilitate the establishment of introduced species, which are often adapted to nutrient-rich soils.

Overall, plant community changes associated with the *C. pubescens* invasion in the vegetation zones of Santa Cruz Island in Galápagos appear to represent a new stable state of the highlands plant communities. The same is probably true for Hawai'i and Tahiti. Due to its ability to vigorously regenerate sexually and asexually, it seems unlikely that *C. pubescens* will be replaced over time as a part of succession following disturbance. The relatively long persistence of *C. pubescens* on the islands where it has been introduced does not suggest the invasion to be an ephemeral one. However, more research is needed on all the invaded oceanic islands in order to address this question.

Animals are also affected by the invasion of *C. pubescens* in Galápagos. For instance, Shriver et al. (2011) found a 31 % reduction in the abundance of the Galápagos rail *Laterallus spilonotus* Gould between 2000 and 2007 and relate this to the increasing *C. pubescens* cover in the study area. These results confirm those of an earlier study that showed reduced rail

populations in *C. pubescens* invaded areas (Gibbs et al. 2003). It is also suspected that the Galápagos petrel *Pterodroma phaeopygia* Salvin is adversely affected by habitat loss as *C. pubescens* overgrows the petrel colonies (Wiedenfeld and Jiménez-Uzcátegui 2008).

Beneficial

In Galápagos, *C. pubescens* may provide a new habitat for epiphytes like locally rare epiphytic fern and orchid species which occur on *C. pubescens* trees covered by old lichens and liverworts (Jäger et al. 2007). In abandoned eucalyptus and pine forests in Hawai'i, both the total number (including non-natives) and the number of endemic species are higher in invaded compared to non-invaded plots (Fischer et al. 2009). This observation was ascribed to *C. pubescens* (and *C. calisaya* Wedd.) adding an additional vegetation layer to the simplified ecosystem (Fischer et al. 2009). In both cases, it seems that the trees change the microclimate towards a more humid environment and thus facilitate the establishment of hygrophilous species, especially ferns. However, these were short term studies and the results may change over time and with an increasingly severe *C. pubescens* invasion.

From a medicinal and economic point of view, alkaloids extracted from *C. pubescens* (and other species, like *C. calisaya*) are commercially valuable (Andersson 1998, Franckenpohl 2000). The most important alkaloid is quinine, which was used for the prevention and treatment of malaria prior to the chemical synthesis of quinine in 1944 (Woodward and Doering 1945, Chopra and Peter 2005). However, the evolution of strains of malaria parasites resistant to the synthetic drugs has revived interest in natural quinine and in the antimalarial properties of the other alkaloids of *Cinchona* (Husain 1991, Gal 2006). This, coupled with the increasing use of the alkaloid quinidine as an antiarrhythmic compound, has increased the demand for *Cinchona* bark (Husain 1991).

The wood of *C. pubescens* is now increasingly used for house and fence construction in Galápagos, since alternative wood (like *Piscidia carthagenensis* Jacq. or *Cedrela odorata* L.) is becoming scarce due to governmental regulations and overexploitation (Jäger pers. obs.).

Regulatory Aspects

Cinchona pubescens is included among the 100 of the worst invaders worldwide (ISSG 2013) due to its rapid spread and detrimental impact on plant and animal species in the Pacific region. In Tahiti, *C. pubescens* is one of 35 invasive plant species that have been declared “threatening to biodiversity” by the Polynesian Government (LEXPOL 2013). “These plants are subject to a ban on new imports, propagation and planting, and prohibition of transfer from one island to another of any whole plant, fragment of plant, cutting, fruit or seed. Their destruction is permitted” (ISSG 2013). In Galápagos, spread to other islands, which would provide highly suitable growing conditions for it (e.g. San Cristóbal, Isabela, Floreana), is prevented by the quarantine protocol for travels between islands (Galápagos National Park Directorate 2014). Starr et al. (2003) state that *C. pubescens* should not be further sold or planted in the Hawaiian Islands. In addition, it has received a High Risk designation by the Hawai’i Weed Risk Assessment program, which is used to help guide planting choices (<http://www.plantpono.org/hpwra-plant.php?id=319>, F. Starr, pers. comm. 2013).

GEOGRAPHICAL DISTRIBUTION

Cinchona pubescens has the broadest natural distribution of all *Cinchona* species, ranging from Costa Rica to Bolivia (Andersson 1998). It has been cultivated in many countries for the production of quinine, mainly in Bolivia, China, Colombia, Costa Rica, the Democratic Republic of Congo, Guatemala, India, Indonesia (Java and Sumatra), Jamaica, Kenya, Mexico, Rwanda, Sri Lanka, Taiwan and Tanzania; it is still grown in some of these locations (Popenoe 1949,

Husain 1991, Andersson 1998, Franckenpohl 2000, Zhengyi et al. 2013). Some of these introductions were only short-lived, like the ones to Algeria and Honduras (Sinclair and Fyfe 1883, Schumann 1891, Popenoe 1949) or to the Southern United States (Fosberg 1947). Surprisingly, *C. pubescens* is now considered rare and endangered in its native range in Ecuador (Günter et al. 2004).

[Insert Table 1]

HABITAT

Climatic requirements and limitations

The ability of *C. pubescens* to tolerate a wide range of environmental conditions probably makes it the most wide-spread of all *Cinchona* species, as well as a successful invader. Its natural distribution seems to be restricted to humid areas with an annual rainfall of >1400 mm (Garmendia 2005). In Galápagos, *C. pubescens* withstands standing water accumulated through heavy rain fall during the El Niño (Jäger pers. obs.. 1998) as well as prolonged dry periods (Itow 2003). Seeds tolerate both shady and sunny conditions for germination (Itow 2003, Figure 8). However, it appears that *C. pubescens* does not occur below 130 m and above 3,300 m above sea level (Gibbs 1885, Andersson 1998, Rentería 2002, Missouri Botanical Garden 2014). Neither does it seem to flourish below 8 °C, whereas it can endure temperatures as high as 33 °C in India and Galápagos (Chopra and Peter 2005, Jäger unpubl. data). In the Pacific region, the distribution of *C. pubescens* ranges from 600–1,400 m in Tahiti (Vanquin 2006), from 180–860 m in Galápagos (Rentería 2002) and from 792–1,158 m on Maui (Starr et al. 2003). In West Java, it occurs at approximately 1,600 m (Junaedi and Mutaqien 2010). Precipitation for optimal growth ranges from 1,500 – 4,000 mm yr⁻¹ in Hawai'i (Fischer 2007), 2,350 – 5,000 mm yr⁻¹ in Tahiti (Vanquin 2006) and averages 1400 mm yr⁻¹ in Galápagos (Jäger and Kowarik 2010).

Habitat and resource requirements and limitations

Cinchona pubescens thrives in a variety of habitat types, which helps to explain its success as an invader. It grows in steep gorges that are difficult to access and in disturbed habitats in its native range in Ecuador (King 1880, Acosta Solís 1945a), as well as in river bottoms, pasture fields and abandoned clearings (Steere 1945). In its introduced range in Hawai'i, Tahiti and Galápagos, it grows especially well in areas that are disturbed and difficult to access (Starr et al. 2003, Vanquin 2006, Jäger and Kowarik 2010). In Ecuador, roots are often exposed to the air (Acosta Solís 1945a), which is also the case in Galápagos, where it thrives in shallow soils less than 20 cm deep (Jäger unpubl. data). *Cinchona pubescens* grows well in a range of soil types, such as volcanic soils, which are rich in organic matter, nutrients and metal oxides (Acosta Solís 1945a, Coster 1942, Chopra and Peter 2005, Garmendia 2005, Vanquin 2006, Fischer 2007). However, *C. pubescens* flourishes in Galápagos despite the fact that the soils are poor in nitrogen and phosphorus (Jäger et al. 2013). Here, *C. pubescens* may benefit from increased nutrient uptake due to its association with arbuscular mycorrhizal fungi, which are not so abundant in association with native species (Schmidt and Scow 1986, Jäger et al. 2013).

Ecosystem and community types invaded

Cinchona pubescens most commonly invades moist highland vegetation zones, which match the wet and warm weather conditions of its native range (Acosta Solís 1945a). In Hawai'i, *C. pubescens* has mainly invaded mesic and wet forests, growing in steep gulches and thick understory vegetation (Starr et al. 2003). In Galápagos, *C. pubescens* spread from the agricultural zone, where it was originally planted, into moist upland zones, including the Miconia zone, the semi-tropical forest (dominated by the endemic tree *Scalesia pedunculata* Hook. f.) and the Fern-Sedge zone (Shimizu 1997, Jäger et al. 2007). In Tahiti, *C. pubescens* spread into secondary and

primary rainforests and undisturbed cloud forest (up to 1,400 m on the peninsula of Tahiti Iti, Vanquin 2006), and in West Java it invaded native forests (Junaedi and Mutaqien 2010).

HISTORY

It is notable that 200 years passed between the discovery of the genus *Cinchona* and its cultivation for medicinal use. The reasons for the long delay are likely related to difficulty in cultivating the tree, particularly due to low seed germination rates (Popenoe 1949). Also, the initially abundant supply of wild bark was sufficient to meet early demands in Europe and America (Popenoe 1949).

Cultivated for the quinine of commerce in many tropical countries and islands, *C. pubescens* was planted on Maui in 1868 and later by state foresters on O'ahu, Maui, and the island of Hawai'i in the first half of the 1900s (Starr et al 2003). It had naturalized on the island of Hawai'i by 1978 and on Maui by 1987 (Starr et al. 2003). On Maui, *C. pubescens* is locally abundant in the Makawao Forest Reserve of East Maui in areas where it was originally planted and in plantations of non-native forest trees, as well as along old roads, and in thick native forests (Starr et al. 2003). In Galápagos, *C. pubescens* is so far only present on Santa Cruz Island, where it was introduced in the 1940s by two farmers, as a cash crop (Hamann 1974, Lundh 2006) and had naturalized by 1972 (Hamann 1974). The crop was not economically viable and quinine production never commenced there. It spread from initial plantings and its distribution increased from 4,000 ha in 1987 to 8,500 ha in 1990 and more than 11,000 ha in 2004 (Buddenhagen et al. 2004).

“In Tahiti, *C. pubescens* was first introduced by Pétard (a pharmacist and chemist) and Boubée (then head of the agronomical station of Tahiti) as a medicinal plant in 1938 in two locations (Fautaua Valley at about 480 m and Afaahiti-Taravao plateau between 280 and 620 m above sea level) (J.-Y. Meyer, pers. comm. 2013). In 1945, about 2,000 trees were cultivated in

Fautaua and 375 in Taravao, but the plantations were abandoned around 1951. In 1965, Pétard wrote that the plantations of Fautaua “were left to the bush, and in Afaahiti they were bulldozed and turned into pastureland, except a few hundreds of trees.” (J.-Y. Meyer, pers. comm. 2013). In 1948, a private farmer had also planted 10,000 plants of mainly *C. pubescens* on the Taravao plateau at about 400 m elevation. The plantation was also neglected in 1959. Pétard went back to this plantation in 1969 and noted that “Although the place is invaded by the bush ... some trees reach the enormous height of 10-13 m and many of them bear flowers or fruits...”. He also checked the Fautaua plantation in 1969 where he found “...about fifty *Cinchona succirubra* (syn. for *C. pubescens*)...” (Pétard 1964, 1986, according to J.-Y. Meyer, pers. comm. 2013).

The successful invasion of *C. pubescens* on all of these islands was a slow but continuous one, which is reflected in the long time that passed between the introduction of the species and the recognition that it had become invasive: about 40 years in Galápagos (Ortiz and Lawesson 1987), about 100 years in Hawai’i (Starr et al. 2003) and about 60 years in Tahiti (Vanquin 2006). In Galápagos, it has been assumed that *C. pubescens* requires disturbance to be able to proliferate since it spread after prolonged man-made fires in the highlands in the late 1960s (Kastdalen 1982). However, it is possible that the expansion of *C. pubescens* simply went unnoticed for a long time before it became obvious. Starr et al. (2003) report that *C. pubescens* spreads along bulldozed forest roads in Hawai’i but it seems that “*C. pubescens* does not need bare, open soil or sunny locations (...to spread) and that some of the densest stands are in the shade of forestry planting of eucalyptus” (H. Oppenheimer, pers. comm. 2013). On Maui, it appears that it spreads from the area it was planted, regardless of the surrounding habitat (K. and F. Starr, pers. comm. 2013). There are indications that disturbance facilitated the spread in Tahiti (Vanquin 2006). Here, the initial spread of *C. pubescens* is likely to have been slowed down by competition with the invasive *Miconia calvescens* DC. which produces intense shade, and is

itself shade tolerant (Vanquin 2006). *Cinchona pubescens* has also been reported to occur outside of plantations in Java and Papua New Guinea (Andersson 1998) and outside the Pacific region in Jamaica (Sauer 1988), Guatemala (Martin and Gandara 1945) and on St Helena (Cronk and Fuller 1995).

PHYSIOLOGY

Cinchona pubescens sheds its leaves continuously throughout the year (Cedeño 1990, Rentería 2002). It does not seem to resorb phosphorus from senesced leaves prior to detaching these, resulting in a two-fold higher phosphorus concentration in the senesced leaves compared to mature green leaves (6.04 mg g⁻¹ vs. 3.15 mg g⁻¹, Jäger et al. 2013). A similar pattern was found for *Olearia axillaris* (DC.) F.Muell. ex Benth. in the coastal area of south-western Australia with phosphorus-poor soils (like the ones in Galápagos) and where senesced leaves also contained the double amount of phosphorus compared to green leaves (5.65 mg g⁻¹ vs. 2.94 mg g⁻¹, Hayes et al. 2013). In both cases, a possible explanation for this unusual finding might be arbuscular mycorrhizal fungi associated with both *C. pubescens* and *O. axillaris* which might enhance the phosphorus uptake of their roots (Hayes et al. 2013, Jäger et al. 2013).

A study of root samples collected from *C. pubescens* adult trees in Galápagos showed that roots were highly colonized with arbuscular mycorrhizal fungi (20-100 %) and PCR-analysis revealed that 95.5 % of these belonged to the family Glomeraceae and 4.5 % to the Diversisporaceae (Serrano 2013).

REPRODUCTION

Cinchona pubescens has hermaphroditic flowers which are probably pollinated by insects. Studies to confirm this are lacking but the sweet fragrance of flowers suggests this mode of pollination (Starr et al. 2003). Biological characteristics of *C. pubescens* that make it a successful

invader in its introduced range include its abundant seed production. The youngest seed producing trees observed were 1-2 years old in Tahiti (Vanquin 2006) and 2 years old Galápagos; the latter were 1.8 m in height with a DBH of 1.5 cm (Jäger unpubl. data). As in the native range (Garmendia 2005), *C. pubescens* trees in Galápagos develop flowers more or less all year round but with a peak between August and November (Rentería 2002). Fruit production peaks between November and April but mature fruits persist on the trees for a long time so that they can be found during all months of the year (Rentería 2002). Development from the opening of the flower to the production of mature fruits takes about 19 weeks (Rentería 2002). Similar observations are reported from India, where flowers and fruits are found almost all year round (Kuntze 1878) but trees only flower after the fourth year (Chopra and Peter 2005). In Galápagos, each capsule contains about 60–70 seeds (J. L. Rentería, pers. comm. 2013) and the thousand-seed weight is 0.26 g (Jäger unpubl. data). A *C. pubescens* tree in Bolivia produces about 7–9 kg of seed per year, which were harvested in November and December during the height of *Cinchona* exploitation (Gibbs 1885).

The light, winged, windborne seeds do not seem to be dispersed far from the parent tree in the introduced range. In Hawai'i, the vast majority of seeds do not reach further than 100 m from the parent tree (Starr et al. 2003) and the maximum dispersal distance reported from Galápagos was about 15 m (Rentería 2002). Another characteristic of *C. pubescens* is the ability of the seeds to germinate in dense understory vegetation as well as under a dense *C. pubescens* canopy, as shown for Hawai'i, Tahiti and Galápagos (Palacios 1993, Meyer 2000, Starr et al. 2003). In addition, *C. pubescens* spreads vegetatively by rapid suckering from roots and stems (Macdonald et al. 1988, Fischer 2007, Jäger et al. 2009).

Since there is limited information available on the germination and growth of *C. pubescens* in the Pacific region, general information is drawn from experimental plantations in

the native and introduced range. In India, seeds sown in soil beds germinate in 10–20 days, with a germination rate from 50 to 85 %. These seedlings usually grow a pair of leaves within three months and grow to a height of about 20–25 cm after 16 months (Joy et al. 2001, Chopra and Peter 2005).

Apparently, introduced *C. pubescens* grows better in the field than under greenhouse conditions. The reasons for this include different nutrient and climate regimes (Jäger unpubl. data). In a greenhouse experiment in Loja, Ecuador, seeds of *C. pubescens* from the native range in Loja germinated after 19 days and reached a total germination rate of 95 % whereas seeds from Galápagos germinated after 17 days with 87% total germination (Jäger and Apolo unpubl. data). Seedlings grown in the greenhouse from Galápagos seeds grew about 13 cm in 13 months, which contrasts with field observations indicating that seedlings grew about 1 m during the first year, attaining about 1.8 m height at the end of the second year (Jäger unpubl. data). Seedlings in a Jamaican plantation also grow about 1 m per year (Sinclair and Fyfe 1883).

Seeds from India begin to lose their viability after six to eight weeks and lose it completely after one year (Kuntze 1878). In Galápagos, seeds also lose their viability after approximately one year (Rentería 2002).

POPULATION DYNAMICS

Cinchona pubescens is a fast growing species in its introduced range. In Tahiti, trees grow about 1-2 m per year and a 10-year old tree reaches a DBH of 5 cm (Vanquin 2006). Trees 15 m tall with a DBH of 25 cm were observed in Galápagos (Shimizu 1997, Jäger unpubl. data). As early as 1974, the invasive character of *C. pubescens* was visible in the highlands of Santa Cruz Island in Galápagos (Hamann 1974). Figure 7 shows the increase of *C. pubescens* density from 1987 to 2005. In 1987, *C. pubescens* density was estimated at 1–100 individuals ha⁻¹ (MacDonald et al. 1988). In the area towards the top of the island, where Macdonald et al. (1988) had counted 1

individual ha^{-1} , about 60–100 individuals ha^{-1} were recorded only four years later (Valdebenito 1991). This rapid increase in density of *C. pubescens* was confirmed by a 7-year study in the fern-sedge highland vegetation (Jäger et al. 2009). Results showed that the density of trees larger than 1.5 m increased from 123 in 1998 to 439 per ha^{-1} in 2005. Concurrently, the number of stems ha^{-1} increased from 355 to 1,652, which represents an average number of stems of 2.9 and 3.8, per tree, respectively. These results parallel those of Shimizu (1997), who recorded an average of 3.4 stems per tree in an area nearby. The basal area increased from 1.0 to 4.2 $\text{m}^2 \text{ha}^{-1}$, while mean *C. pubescens* cover increased from 6.6 % to 16.4 % over 7 years (Jäger et al. 2009). The highest *C. pubescens* cover recorded in individual 20 × 20 m plots was 42 % (Jäger et al. 2009).

[Insert Figure 7]

Cinchona pubescens reaches similar abundance levels on other Pacific islands. In experimental plots on the Taravao plateau and on the Atar Mountain in Tahiti (600–955 m above sea level), the maximum percentage cover of *C. pubescens* was 55 %, maximum density of stems was 9,200 ha^{-1} and that of seedlings was 14,500 ha^{-1} (Vanquin 2006). However, these densities were recorded from small study plots in the most invaded areas of Tahiti and may not necessarily be representative of the current situation (J.-Y. Meyer, pers. comm. 2013). In abandoned eucalyptus and pine plantations, as well as in natural *Acacia koa* stands in the Makawao Forest Reserve on Maui, Hawai'i, average percentage cover of *C. pubescens* reached 27%, the average density of stems (0.2–1 m) 4,000 ha^{-1} and that of seedlings 114 ha^{-1} (Fischer 2007). Population density in the Patengan Natural Reserve in the tropical mountain rainforests of West Java was

222 individuals ha⁻¹, which is the highest density of tree population in all three research locations around Mount Patuha (Junaedi and Mutaqien 2010).

RESPONSE TO MANAGEMENT

Cinchona pubescens has long been recognized as a potential risk to native vegetation in its introduced range, especially in Hawai'i, Galápagos, and Tahiti. On Santa Cruz Island, several control methods to combat *C. pubescens* have been implemented in Galápagos National Park and in the agricultural area. Manual methods include felling and uprooting of trees as well as hand-pulling of smaller plants, but trees re-sprout from cut stumps (Macdonald et al. 1988, Buddenhagen et al. 2004, Figure 8). Chemical control methods consist of applying herbicides by a range of means such as hack and squirt, basal bark, cut stump, girdle and squirt, branch filling, tree injections, and foliar spraying (Buddenhagen et al. 2004). Most of these methods were ineffective in the long run. Eventually, a hack and squirt technique was developed where a mixture of picloram and metsulfuron was applied to connecting machete cuts around the circumference of tree trunks, killing 73-100% of the trees (Buddenhagen et al. 2004, Figure 8). Smaller shoots and saplings were pulled out by hand. This method is now being successfully applied for *C. pubescens* control by the Galápagos National Park Service on a small scale (approximately 110 ha between 1998 and 2003, Buddenhagen and Yánez 2005) in addition to uprooting trees in conservation priority areas (Jäger and Kowarik 2010).

Studies on the impacts of these measures revealed that despite an initial decline in species cover, native plants recover and total species cover as well as species diversity increases after the control action occurred (Jäger and Kowarik 2010, Jäger unpubl. data). However, both control actions caused severe disturbance to the surrounding vegetation and soil (Figure 8). This probably also facilitated the establishment of other introduced species. For example, there was a significant increase in cover of the highly invasive blackberry, *Rubus niveus* Thunb. (Jäger and

Kowarik 2010, Jäger unpubl. data). In addition, continuous hand-pulling of emerging seedlings over a long period would be necessary to guarantee lasting control success (Jäger and Kowarik 2010).

Buddenhagen and Yáñez (2005) estimated the costs for the chemical control of *C. pubescens* on Santa Cruz Island at between US\$14–2,225 ha⁻¹, depending on stem density. Treating all existing plants in the invaded area of at least 11,000 ha once would require about 276,500 man-hours (equivalent to 150 men working for a year) at an estimated cost of US\$1.65 million in 2005 (Buddenhagen and Yáñez 2005). Treated areas would still have to be re-visited subsequently for several years to pull out germinating seedlings (Jäger and Kowarik 2010).

[Insert Figure 8]

Control of *C. pubescens* is difficult in Hawai'i (mainly Maui), since it primarily grows in steep gulches and thick understory vegetation. On the other hand, controlling small populations in patches of native vegetation could prevent further spread and help slow down the degradation of the remaining native forest in the area (Starr et al. 2003). An interesting method was recently developed to kill invasive *Miconia calvescens* DC. in inaccessible areas in Hawai'i by shooting encapsulated herbicide projectiles at *Miconia* plants from a helicopter (Leary et al. 2013). Something similar might be possible for *C. pubescens* in Hawai'i and elsewhere.

NATURAL ENEMIES

Although the databases of the Systematic Mycology and Microbiology Laboratory (Farr and Rossman 2010) list 27 fungi species as associated with *C. pubescens*, only seven of these occur in the native range of *C. pubescens* (e.g. *Elsinoe cinchonae* Jenkins, *Phytophthora cinnamomi* Rands, *Prillieuxina cinchonae* J.A. Stev.). The scab-causing pathogen *Elsinoe cinchonae* Jenkins

was also recorded from *C. pubescens* from western Ecuador (H.C. Evans, pers. comm. 2013). However, there is no evidence that these species are important economic pathogens (PIER 2014) and therefore might not be likely candidates for biological control.

In plantations in Guatemala, India, and Java, *Cinchona* is susceptible to many pests and diseases. *Cinchona* seed beds are frequently affected by the fungi *Rhizoctonia solani* J.G. Kühn, *Phytophthora* spp. (root rot fungus), and *Rosellinia arcuata* Petch (black-root fungus), causing a disease known as “damping off” (Coster 1942, Popenoe 1949, Chopra and Peter 2005). These fungi penetrate the seedlings through their roots and cause sudden wilting and rotting of seedlings. In Java and India, plants are also attacked by the insects *Helopeltis* (tea mosquito) and *Pachypeltis* (leaf scorch) (Coster 1942, Chopra and Peter 2005). *Cinchona* stem bark disease due to *Phytophthora cinnamomi* Rands is a major disease in central African countries (Rwanda and the Democratic Republic of Congo, Chopra and Peter 2005). In Galápagos, secondary pathogens were isolated from *C. pubescens*, mainly *Fusarium* spp. and *Botryodiplodia theobromae* Pat. (H.C. Evans, pers. comm. 2013). Vanquin (2006) reports that in 1939, Roger Heim found a mushroom of the Agaricaceae family in Papua New Guinea that attacks the roots of *C. pubescens* which leads to a desiccation of the seedlings and a partial destruction of different plant parts.

For a detailed description of the natural enemies of *C. pubescens* see the CABI Invasive Species Compendium (CABI 2014).

PROGNOSIS

An interval ranging from 40-100 years passed before *C. pubescens* was recognized as an invasive species after its initial naturalization in Tahiti, Hawai'i and Galápagos. One possible reason for this could be that the area lacked openings for invasion windows (“safe sites”) in the form of disturbance or climate change (Kowarik 1995). Alternatively, the invasion may have simply been unnoticed for several decades. Starr et al. (2003) state that other mesic and wet

forests on Maui currently free of *C. pubescens* are potentially threatened by invasion in the future. A future expansion is also possible on Tahiti (Vanquin 2006). In addition, *C. pubescens* has been reported to occur outside of plantations in Papua New Guinea and Jamaica (Sauer 1988, Andersson 1998). This means that there is still a risk that *C. pubescens* might become invasive in areas where it has been introduced but its ability to spread without human intervention has not yet been recognized. For example, *C. pubescens* was introduced to Java in 1856 (de Padua et al. 1999) but it was only recently considered invasive (Junaedi and Mutaqien 2010). In Galápagos, *C. pubescens* could easily grow on islands other than Santa Cruz which receive enough rainfall to allow agriculture, like San Cristóbal, Isabela and Floreana, if seeds were brought there by humans. The same is probably the case for the Hawaiian Islands. *Cinchona pubescens* produced a score 9 (high risk) in the Weed Risk Assessment from Pacific Island Ecosystems at Risk (Daehler et al. 2004, PIER 2014) and therefore could become invasive in many islands if introduced and found optimal growing conditions. Popenoe (1945) reports that *Cinchona* seedling in the first plantations in Guatemala died shortly after planting and it was assumed that the soils were not sufficiently acidic. Thus it is possible that *C. pubescens* would more likely become invasive in volcanic (= acidic) soils. As a result, known populations on all Pacific islands as well as in Asia (f. ex. Philippines or Taiwan) should be monitored carefully. In the case of small *C. pubescens* populations, it would be best to eliminate these by control methods currently applied in the Galápagos National Park Directorate.

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Table 1 Geographic distribution of *Cinchona pubescens* in the Pacific region

	Present	Absent	No information	Citation
American Samoa		X		Presumed absent. Not listed in US Forest Service 2014
Australia		X		Presumed absent. Not listed in the Flora of Australia Online 2014
Bonin Islands		X		Resumed absent. Not listed in Kawakami and Okochi (eds.) 2010
Cedros Island, Mexico		X		Presumed absent. Not listed in Oberbauer 1993
Clarion Island, Mexico		X		Presumed absent. Not listed in Mueller-Dombois and Fosberg 1998
Clipperton Island		X		Presumed absent. Not listed in Sachet 1962
Cocos Island, Costa Rica		X		Presumed absent. Not listed in Fosberg and Klawe 1966
Cook Islands		X		Presumed absent. Not listed in US Forest Service 2014
Easter Island (Isla de Pascua or Rapa Nui)		X		Presumed absent. Not listed in Dubois 2013
Fiji	X*			Kew Gardens 2013 (but see US Forest Service 2014)
French Polynesia				
Austral Islands		X		Presumed absent. Not listed in DIREN 2007
Marquesas		X		Presumed absent. Not listed in Wagner et al. 2002
Society Islands	X			On Tahiti (Meyer 2004)
Tuamotu Islands		X		Presumed absent. Not listed in DIREN 2007

Galápagos Islands	X			Hamann 1974
Gorgona Island			X	
Guadalupe Island, Mexico		X		Presumed absent. Not listed in Oberbauer 2005
Guafo Island, Chile			X	Presence unlikely, given the low annual temperatures
Hawaiian Islands	X			Starr et al. 2003
Henderson Island, Chile		X		Presumed absent. Not listed in Waldren et al. 1995
Indonesia	X			On Java (Andersson 1998)
Isla de la Plata, Ecuador			X	Presence unlikely, given the semiarid climatic conditions
Japan (main islands)	X**			On Okinawa (Nagumo et al. 2010)
Juan Fernandez		X		Presumed absent. Not listed in Cuevas et al. 2004 or Greimler et al. 2013
Kiribati				
Gilbert Islands		X		Presumed absent. Not listed in Wagner et al. 2012
Line Islands		X		Presumed absent. Not listed in Mueller-Dombois and Fosberg 1998
Phoenix Islands		X		Presumed absent. Not listed in Pierce and Brown 2008
Lobos Islands, Peru			X	Presence unlikely, given the arid climatic conditions
Lord Howe Island		X		Presumed absent. Not listed in the Flora of Australia Online 2014
Malpelo Island, Colombia			X	Presence unlikely, given the arid climatic conditions
Micronesia				
Caroline Islands	X***			Wagner et al. 2012
Mariana Islands (including Guam)		X		Presumed absent. Not listed in US Forest Service 2014
Marshall Islands (including Wake Island)		X		Presumed absent. Not listed in US Forest Service 2014 or Wagner et al. 2012
Nauru		X		Presumed absent. Not listed in US Forest Service 2014
Palau	X****			Fosberg et al. 1993 (but see US Forest Service 2014)
New Caledonia		X		Presumed absent. Not listed in Beauvais et al. 2006
New Guinea			X	
New Zealand		X		Presumed absent. Not listed in Breitwieser et al. (eds). 2010
Niue		X		Presumed absent. Not listed in Space and Flynn 2000

Norfolk Island		X		Presumed absent. Not listed in the Flora of Australia Online 2014
Pacific Equatorial Sporades (Baker, Howland and Starbuck Island)		X		Presumed absent. Not listed in Mueller-Dombois and Fosberg 1998
Palmyra			X	Presence unlikely, given the climatic conditions.
Papua New Guinea	X			Andersson 1998
Philippines	X			FAO 2013
Pitcairn Island		X		Presumed absent. Not listed in Kingston and Waldren 2003
Sala y Gomez		X		Presumed absent. Not listed in Mueller-Dombois and Fosberg 1998
Samoa		X		Presumed absent. Not listed in Mueller-Dombois and Fosberg 1998
Socorro Island		X		Presumed absent. Not listed in Mueller-Dombois and Fosberg 1998
Solomon Islands		X		Presumed absent. Not listed in Mueller-Dombois and Fosberg 1998
Taiwan	X			Zhengyi et al. 2013
Tokelau Island		X		Presumed absent. Not listed in Mueller-Dombois and Fosberg 1998
Tonga		X		Presumed absent. Not listed in US Forest Service 2014
Tuvalu		X		Presumed absent. Not listed in Mueller-Dombois and Fosberg 1998
Vanuatu		X		Presumed absent. Not listed in Mueller-Dombois and Fosberg 1998
Wallis and Futuna		X		Presumed absent. Not listed in Mueller-Dombois and Fosberg 1998

*Only a single collection record from Kew Gardens, collected in 1868 by the Colonial & Indian Exhibition, Fiji Commission

** Nagumo et al. 2010 mention the establishment of *Cinchona* plantations on Okinawa and Kagoshima in 1876 but do not mentioned which species. Plants had died by 1884.

***Listed as *Cinchona succirubra*

****Introduction reported but not confirmed

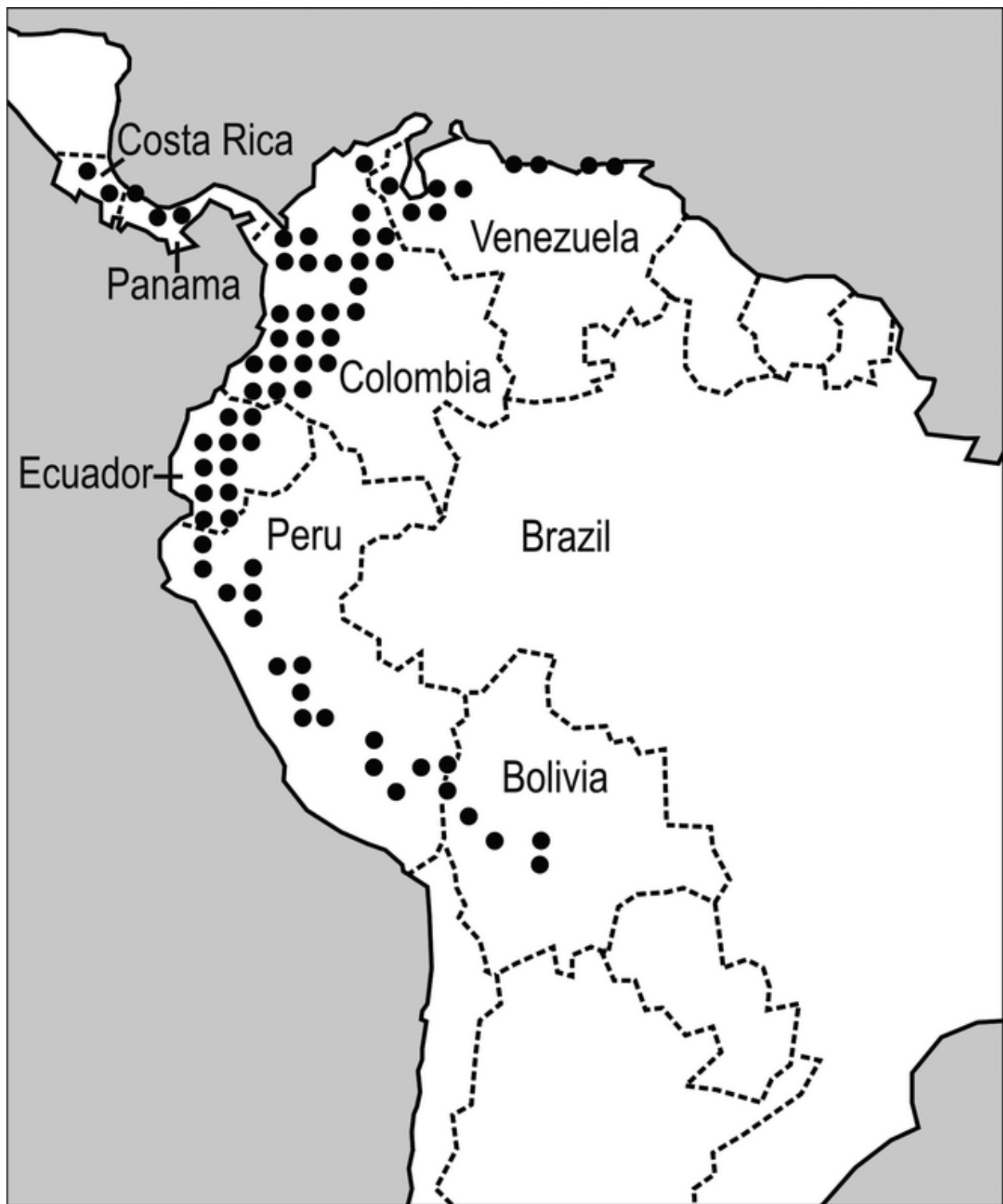


Figure 1. Natural distribution of *Cinchona pubescens* (modified after Andersson 1998, Heinke Jäger: *Cinchona pubescens*. Enzyklopädie der Holzgewächse. 2011. Volume 58, pp 14. Copyright Wiley-VCH Verlag GmbH & Co. KGaA. Reproduced with permission).



Figure 2. Growth form of *Cinchona pubescens* in the fern-sedge vegetation on Santa Cruz Island, Galápagos (note invasive *Psidium guajava* trees in the surroundings, H. Jäger)



Figure 3. Invasion of *Cinchona pubescens* in fern-sedge vegetation on Santa Cruz Island, Galápagos (H. Jäger)



Figure 4. *Cinchona pubescens* invaded habitats. *Left*: *Acacia koa* forests in the Makawao Forest Reserve on Maui, Hawai'i (L. Fischer); *right*: Atara Mountain on Tahiti (J.-Y. Meyer).

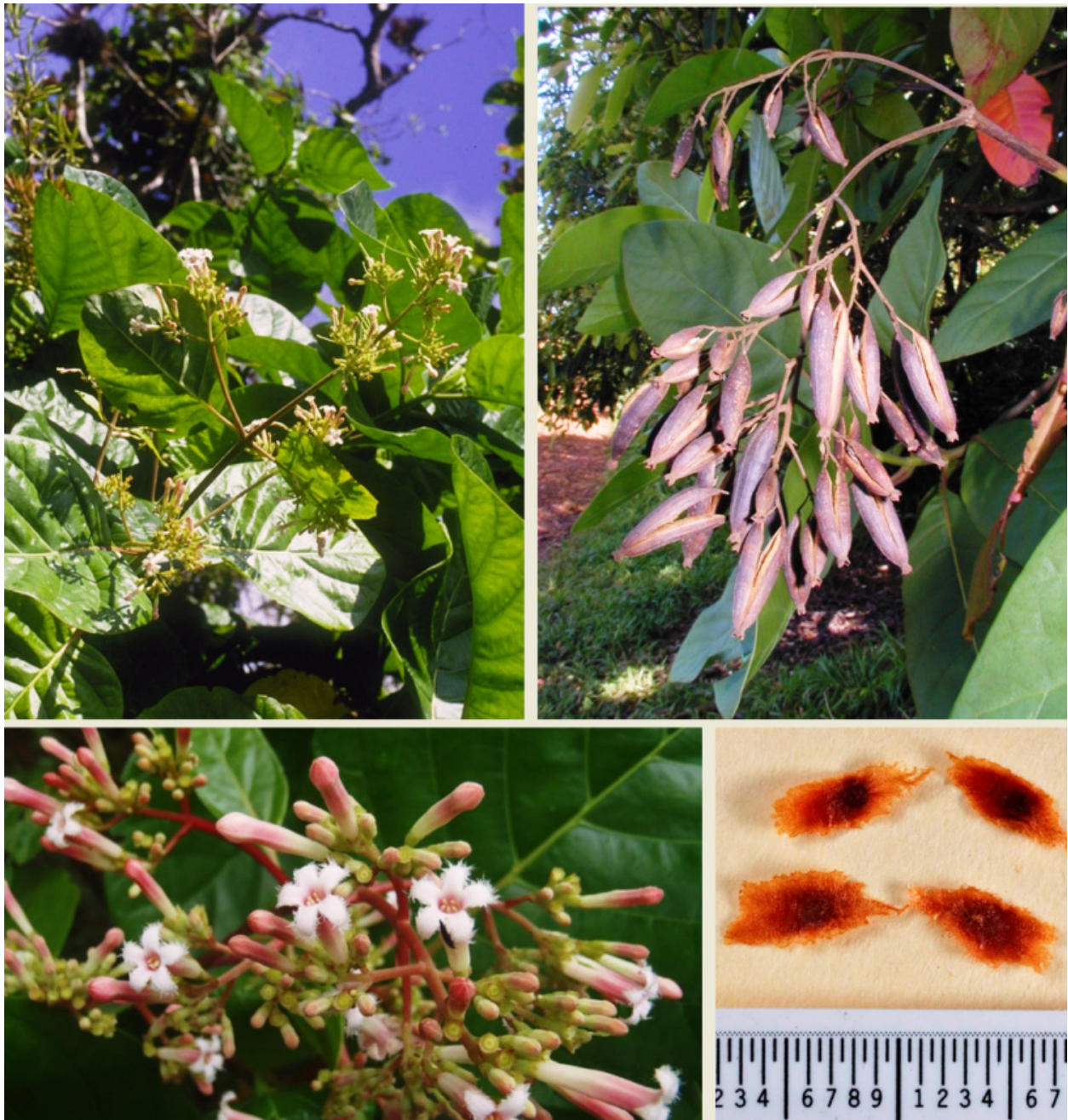


Figure 5. *Cinchona pubescens* morphology. *Top left*: inflorescence and leaves on Santa Cruz Island, Galápagos (H. Jäger); *top right*: fruits from the Taravao plateau, Tahiti (J.-Y. Meyer); *bottom left*: flowers on Santa Cruz Island, Galápagos (H. Jäger); *bottom right*: seeds on Santa Cruz Island, Galápagos (cm scale, two long vertical bars is 1 cm, F. Bungartz).

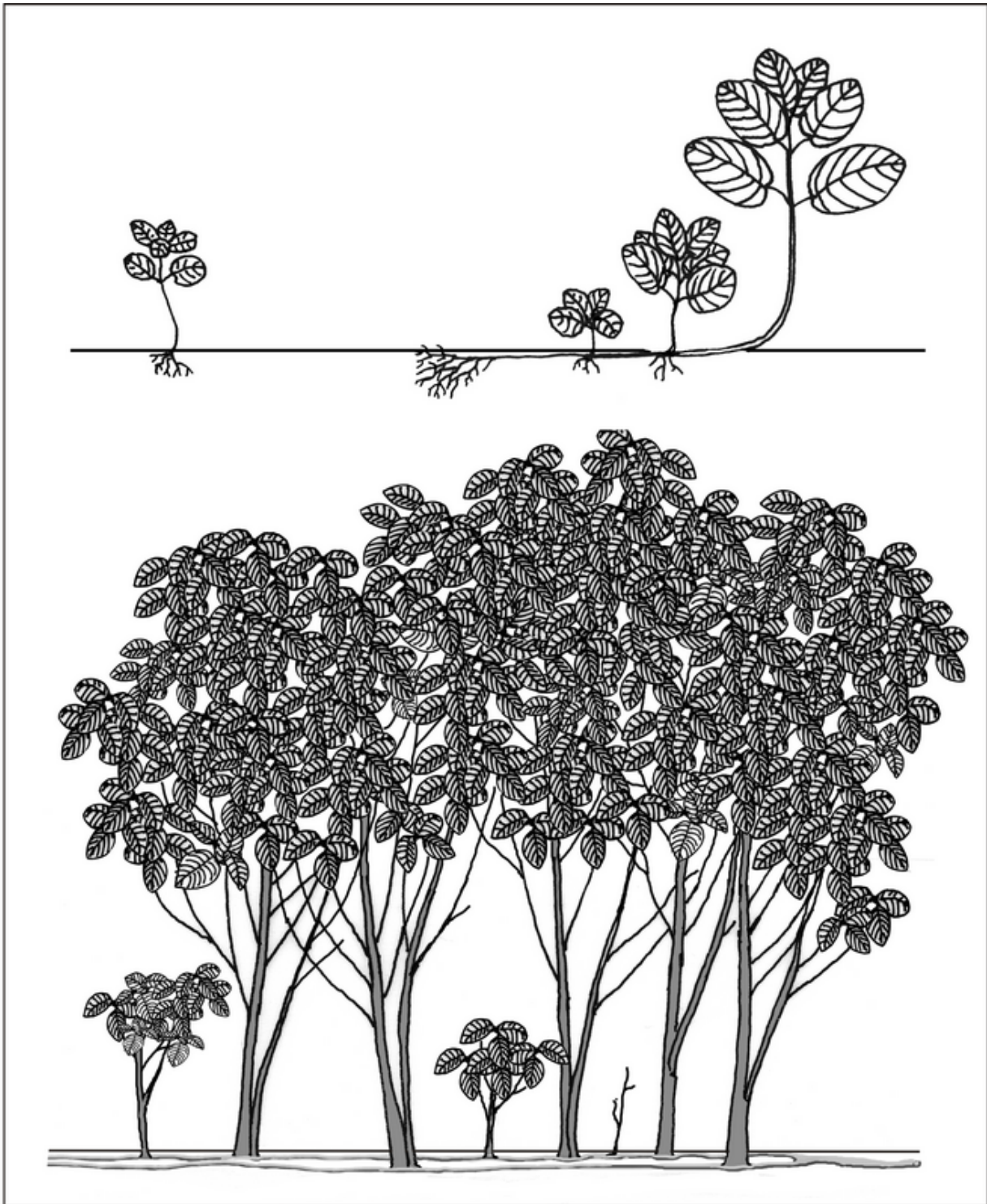


Figure 6 Growth form of *Cinchona pubescens* in Galápagos (modified after Shimizu 1997. Heinke Jäger: *Cinchona pubescens*. Enzyklopädie der Holzgewächse. 2011. Volume 58, pp 14. Copyright Wiley-VCH Verlag GmbH & Co. KGaA. Reproduced with permission).

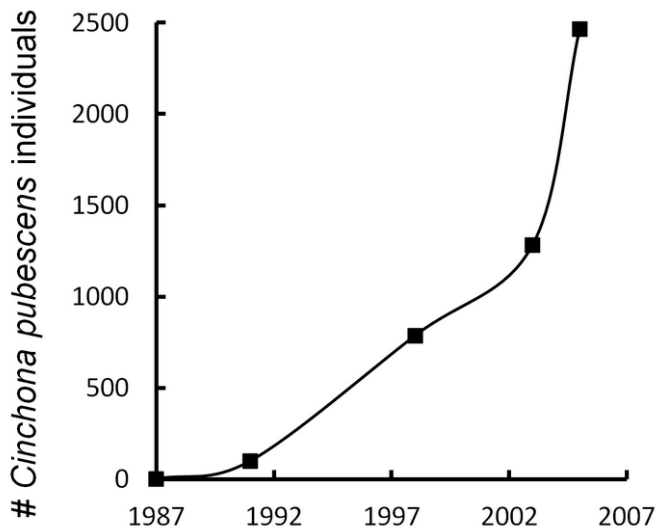


Figure 7. Increase of *Cinchona pubescens* individuals (including seedlings) at Media Luna between 1987 and 2005, on Santa Cruz Island, Galápagos. Value for the year 1987 from Macdonald et al. 1988, for the year 1991 from Valdebenito 1991, and for the years 1998 to 2005 from Jäger et al. 2009.



Figure 8. *Cinchona pubescens* regeneration and control. *Top left*: germination under dense *Miconia robinsoniana* vegetation; *top right*: resprouting after manual control; *bottom left*: chemical control ('hack and squirt'), *bottom right*: manual control. All photos taken by Heinke Jäger on Santa Cruz Island, Galápagos.

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