Cinchona pubescens Vahl, 1790

syn.: Cinchona chomeliana Wedd., 1848,
Cinchona lutea Pav. in Howard, 1859,
Cinchona ovata (Ruiz & Pavon, 1799),
Cinchona succirubra (Pav. ex Klotzsch, 1857)[1]

Red cinchona, Red quinine tree, Peruvian bark,
Jesuits' bark, Countess bark — Family: Rubiaceae

Dutch: Kinaboom
French: arbre à quinine, quinquina rouge
German: Chinarinde, Chinarindenbaum
Spanish: Cascarilla, Hoja ahumada, Hoja de zambo, Quina[2]

Fig. 1: Cinchona pubescens trees in the introduced range: highlands of Santa Cruz Island Galápagos (600 masl)

[1] For a list of synonyms see Andersson (1998)
[2] Acosta Solís (1945b) lists 18 different common names for Ecuador alone
[3] Author's note: Since C. succirubra and C. ledgeriana are synonyms for C. pubescens and C. calisaya, respectively, these names are substituted throughout the text when synonyms were used in older publications

Cinchona is the most commercially important genus of the family *Rubiaceae* (coffee family) after the genus *Coffea*, which produces the coffee of commerce. The genus *Cinchona* comprises 23 species of tropical evergreen trees and shrubs, which are distributed from Costa Rica to Bolivia. *C. pubescens* grows at altitudes between 300 and 3300 m. It is a tree with broad leaves and white or pink fragrant flowers arranged in clusters. *C. pubescens* has been cultivated in several tropical regions of the world for its quinine-containing bark and roots. Quinine was used as a remedy to treat malaria and therefore had significant economic importance from the 17th to the beginning of the 20th century. In 1944, quinine was synthesized and therefore *C. pubescens* lost much of its importance, but natural quinine is still used both where the synthetic is not available and for other medicinal purposes.

The genus *Cinchona* was named after the Countess of Chinchón, wife of the Viceroy of Peru, by the Swedish botanist Linnaeus in 1742. According to the well cited legend, the countess was cured of malaria by having been administered the bark of *Cinchona* in 1638 after all other remedies failed. Although this story is not true, *Cinchona* ever since was frequently used as a malaria remedy, especially distributed by the Jesuits in their world travels. *Cinchona* is the national tree of Ecuador and is on the coat of arms of Peru.

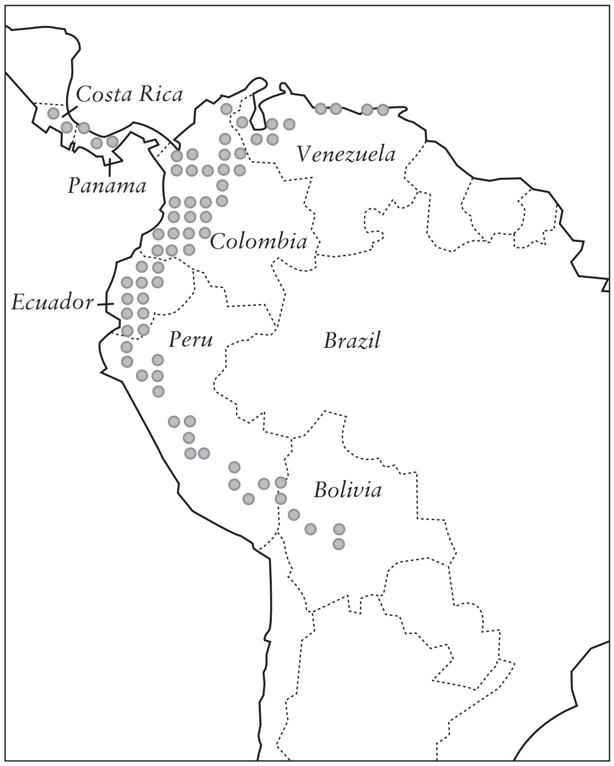

Fig. 2: Natural distribution of Cinchona pubescens (drawing by W. Roloff, modified after Andersson 1998)

Distribution

C. pubescens has the widest natural distribution of all *Cinchona* species, from the mountainous area of central Costa Rica and Panama and the coastal zone of NE Venezuela, over the Andean ridge through Colombia, Ecuador and Peru, and south to central Bolivia at altitudes between 300 and 3300, where it was also traditionally cultivated [2, 7].

Due to the massive exploitation of quinine in past centuries, this formerly common tree of the western Andean slopes was exploited to the point of extinction in its native range [5]. The *C. pubescens* forests had almost disappeared as early as 1859 in Ecuador [62] and elsewhere [64].

The genus *Cinchona* was introduced to other tropical regions mainly for the production of quinine. *C. pubescens* is known to have been cultivated (and is still being cultivated) in e.g. India, Indonesia, some African countries, Sri Lanka, and Mexico [7]. It was also introduced to some Pacific islands and archipelagos, like Galápagos, Hawaii, and Tahiti, where quinine was never exploited and where the species has become highly invasive [37, 50, 66]. Here, its distribution ranges from 600 to 1400 m in Tahiti [65], from 180 to 860 m in Galápagos [56], and from 792 to 1158 m on Maui [63].

Morphology

In its native range, *C. pubescens* is an evergreen tree of 10–25 m height and a diameter at breast height (DBH) of 20–80 cm [3, 7] in Ecuador, and 30 m height and a DBH of 90 cm in northern Peru [31]. In Ecuador, the trees usually have a main trunk that ramifies in the upper third and has a semicircular crown [3].

In its introduced range, e.g. in Galápagos, trees can reach a height of 15 m and a DBH of 25 cm ([61], H. Jäger, unpubl. data). They have a main trunk but also often develop several equally strong trunks a short distance away from the original trunk, which emerge by suckering of specialized underground stems (cf. [15]). In this way, *C. pubescens* trees take on a multi-stemmed growth form, with the individual stems still connected [61]. In addition, it resprouts from fallen and cut stems to produce vertical shoots. Contrary to its habit in its natural range in Ecuador, in Galápagos the tree produces branches already in the lowest third of the trunk, which are slightly bent upwards, resulting in a semicircular to cylindrical crown (H. Jäger, pers. observ.). This observation contradicts that of Shimizu [61] who reported that young trees produce horizontal branches in Galápagos. In Tahiti, *C. pubescens* reaches a height of 14 m and a DBH of 30 cm, but most trees have a DBH below 10 cm [65].

Leaves, leaf coloring

C. pubescens is characterized by its membranous, large, broad leaf blades with a thin cuticle. Leaves are opposite, 8.3–23 cm long and 5.3–21 cm wide (those of saplings and other rapidly growing shoots often much larger than those of flowering shoots), elliptic or ovate to suborbicular with pubescent petioles (1.2–5 cm long) and stipules (1.2–2.6 × 0.5–1.5 cm) [7]. Stipules are often caducous and leave a well-marked scar on the branch [3]. Leaf blades are matt above with 7–11 pairs of conspicuous secondary veins, sometimes puberulent along veins, and usually more or less densely hairy beneath, especially on the young leaves. Leaf domatia are usually absent but, if present, they are distinctly pouch-shaped [7]. The leaf morphology is variable though, especially with respect to size, shape, and indumentum of the leaf blades. Reasons for this variation could include local differentiation and clinal variation in response to altitude [3, 34]. This already confusing variation is worsened by hybridization, mainly with *C. calisaya* and *C. macrocalyx* [7]. Leaves turn red with age and are shed continuously and in small quantities throughout the year in Galápagos [10, 56].

Fig. 3: Leaves in Galápagos

Flowers, fruits, and seeds

In Ecuador, around Loja, *Cinchona* flowers and bears fruits at the same time all year round [25]. The flowers of *C. pubescens* are clustered in large, broadly pyramidal panicles, usually up to 20 cm but sometimes longer in size. The corollas are pinkish or purplish, paler at base (corollas outside may be white to light pink or red in Hawaii and Galápagos) and are fragrant [7, 63]. It was thus assumed that *C. pubescens* is insect-pollinated but this has not been confirmed anywhere [56, 63]. The corolla tube is 9–14 mm long, pubescent outside and glabrous inside. The capsules are ellipsoid to subcylindrical and 13–41 × 5–7 mm long, opening from the base to tip when mature. Seeds are 7–12 × 2.1–2.8 mm, including the irregularly dentate wings [7]. As in the native range, *C. pubescens* trees in Galápagos develop flowers more or less all year round but with a peak between August and November. Development from the opening of the flower to the production of mature fruits takes about 19 weeks [56]. Highest fruit production is 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 [56]. Each capsule contains about 60–70 seeds (J. L. Rentería, pers. comm. 2004). Similar observations are reported from India, where flowers and fruits are found almost all year round [44]. In India, one gram of *Cinchona* seeds (including *C. pubescens*) contains about 300 to 400 seeds.

Fig. 4: Flower panicles in Galápagos

Fig. 5: Flowers in Galápagos

Fig. 6: Fruits in Galápagos with Ecuadorian 10-cent coin, equal to the size of a US 10-cent coin (ca. 1.8 cm)

Fig. 7: Opened fruits in Galápagos

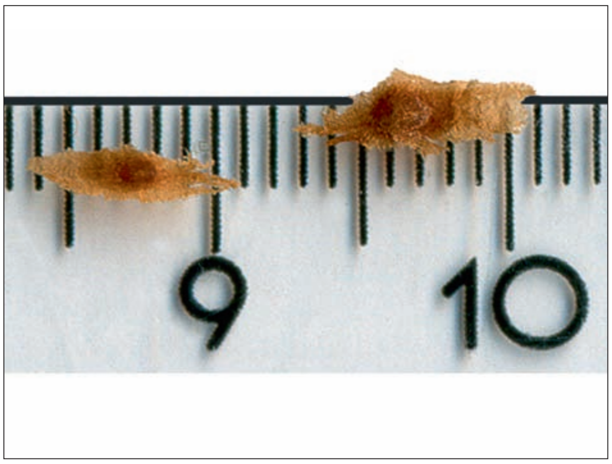

Fig. 8: Seeds (scale is in cm), in Galápagos

Wood and bark

Since the focus of research on *Cinchona* has always been on the quinine content in the bark, there is only little information available on its wood characteristics. In its natural range, the wood of *C. pubescens* is brown-yellowish to brown-orange, compact and of a fine texture [42], and has a density of 0.54 $g\ cm^{-3}$ [11, 69]. The outer bark is 3–20 mm thick and light coffee-brown, turning cinnamon-brown when dry. It may have white streaks caused by lichens growing on it [3, 42]. When the bark is being peeled off the trunk, a milky sap leaks from the cuts and the cortex below takes on a reddish color (hence the name “red bark”), which quickly darkens. The fresh and dry bark has the very bitter taste characteristic for all *Cinchona* species [3].

Roots

In several drawings, Acosta Solís [2] describes adventitious roots of *Cinchona* species in Ecuador as “stilt roots”, which are either covered by the soil or exposed. However, this observation does not concur with observations from Galápagos, where these roots are rather simple and weak [61].

Taxonomy, genetic differentiation, and hybridization

The genus *Cinchona* L. was first described by La Condamine in 1738 [22]. Since this genus was medicinally important, it has historically attracted extraordinary attention from taxonomists. Many different names were established in the 19th century on the grounds of very minor morphological differences [29, 54]. In his revision of the genus *Cinchona*, Andersson [7] considered more than 330 names (including many at variety level) and recognized 23 species. The taxonomy of *C. pubescens* is especially difficult since it frequently hybridizes with other *Cinchona* species where they occur together in nature [3, 7, 9, 29]. This confusion was already noticed by von Humboldt in 1808, who stated that one might consider *Cinchona* leaves from the same branch as being specimens of different species if one did not have the opportunity to see the branch in the wild [34]. In 1946, four species were known to form hybrids with *C. pubescens* [3], whereas Andersson [7] lists 7 species hybridizing with it (*C. barbacoensis*, *C. calisaya*, *C. lancifolia*, *C. lucumifolia*, *C. macrocalyx*, *C. micrantha*, *C. officinalis*). Hybrids between *C. pubescens* and *C. calisaya* are the most commonly found in nature and seem also to have been produced in cultivation [7].

The chromosome number of *C. pubescens* is 2n = 34 [7].

Fig. 9: Tree trunk (overgrown with mosses and liches), in Galápagos

Fig. 10: Part of trunk cut open to show the wood, in Galápagos. Note the red coloration after cutting the trunk, hence the name „red guinine"

Growth, development, and yield

In its natural range in Bolivia, a *Cinchona* tree reaches a height of about 4 m and a diameter of about 15 cm when 6 years old, and over 30 cm in diameter when 10 or 12 years old [23]. *Cinchona* trees in India flower after the fourth year [12], whereas *C. pubescens* trees in Galápagos flower when only 2 years old, with a DBH of 1.5 cm (H. JÄGER, pers. observ.). A *C. pubescens* tree in Bolivia produces about 7–9 kg of seed per season, which are harvested in November and December. In Jamaica, young seedlings of *C. pubescens* grow about 1 m during the first year and reach about 1.8 m at the end of the second year, with a DBH of 3.6 cm [1]. The maximum DBH of *C. pubescens* trees found in Tahiti was 30 cm [65] and 10-year-old trees had a DBH of 5 cm [65].

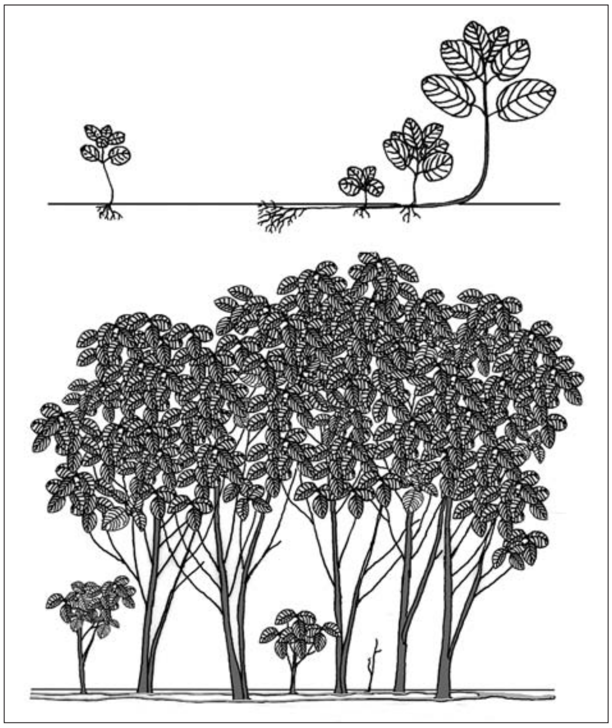

Fig. 11: Growth forms and habitus of Cinchona pubescens in Galápagos (drawing by W. ROLOFF, modified after SHIMIZU 1997)

In Galápagos, *C. pubescens* demography was studied over 7 years in the Fern-Sedge highland vegetation zone of Santa Cruz Island, which is largely invaded by *C. pubescens* [37]. Results showed that the density of *C. pubescens* trees larger than 1.5 m increased from 123 per hectare in 1998 to 439 in 2005. Concurrently, the number of stems per hectare increased from 355 to 1652, which represents an average number of stems per tree of 2.9 and 3.8, respectively. These results parallel those of SHIMIZU [61], who counted 3.4 stems per tree in an area nearby.

At the same time, basal area increased from 1.0 to 4.2 m^2 ha^1, while mean *C. pubescens* cover increased from 6.6 to 16.4 % [37].

In Tahiti, *C. pubescens* reached a maximum density of 9200 stem ha^{-1} and 14,500 seedlings ha^{-1} [65]. However, these data are from small study plots in the most invaded areas of Tahiti (J.-Y. MEYER, pers. comm. 2010).

In Bolivia, the bark of *C. pubescens* is thicker and heavier when older, but does not contain as much quinine. It is stripped between October and January, producing about 2 kg on average [23]. The bark is harvested after 6 to 10 years in Ecuador [3] and after 8 to 12 years in Jamaica [23]. The bark of *Cinchona* in India is harvested after the third or fourth year from trees that are uprooted to thin the plantation. A second harvest can be carried out on the remaining trees after the seventh or eighth year and a final harvest after about 12 years [12]. In commercial *Cinchona* plantations in Peru, 2860 kg of *C. pubescens* bark was harvested between 1943 and 1945 and sold at a price of US $ 109,500 [31].

In Ecuador, naturally occurring *C. pubescens* in the province of Bolívar and on the western slopes of the Andes produces the highest alkaloid content [2, 49]. However, the alkaloid content varies considerably with locality, from 0.1 to 7.8 % [3, 60], and with the age of the tree and the part of the tree the samples were taken from. Younger trees and thicker barks contain more alkaloids [42]. This especially applies to the quinine content, which is up to 5 % in the wild form collected from the slopes of Chimborazo in Ecuador, whereas the wild form from Costa Rica contains hardly any [54]. The bark of trunks, twigs, and roots of cultivated *C. pubescens* in India, Java and Sri Lanka yields between 4–8 % of total alkaloids, of which 0.8–1.4 % is quinine [12, 60]. The alkaloid content of *C. pubescens* in India is highest from the fourth to seventh year and then declines again [12]. The same is true for the alkaloid content for *C. pubescens* cultivated in Bolivia [23]. A 16-year study in Java showed that the quinine content of *Cinchona* clones increased in the early years and then declined again in the fifth or seventh year. Manuring maintained the quinine content or reduced the rate of decline in Java [13]. The quinine content of the bark from the same seedling variety or clone varies with the soil and environmental conditions and can be increased by stunting the vertical growth [13].

In 1891, *C. pubescens* was the species of choice for cultivation and provided the largest amount of bark, especially in Sri Lanka and Java [60]. Nowadays, the main *Cinchona* alkaloid producing countries are Indonesia, the Democratic Republic of Congo, Tanzania, Kenya, Rwanda, Sri Lanka, Bolivia, Colombia, Costa Rica, and India. These countries produce between 400–700 tons of alkaloids obtained from 8000–10,000 tons of bark produced annually [20, 35]. The bark yield in India alone is about 9000–16,000 kg ha^{-1} [39].

Fig. 12: Young seedlings in Galápagos

Fig. 13: Dense C. pubescens stand with native vegetation in the understorey in Galápagos

Regeneration, reproduction, cultivation

Due to the overexploitation of *Cinchona* before the synthesis of quinine in 1944, *Cinchona* species have drastically been reduced in their abundance in South America, e.g. in Bolivia, Colombia and Ecuador [9, 32]. As a consequence, *C. pubescens* is now extremely rare in Ecuador and has a low regeneration rate ([22], C. I. Espinosa, pers. comm. 2010). It used to grow best at an altitude of 850–1350 m, in areas with steep slopes and in disturbed habitats [2]. *C. pubescens* was also cultivated here and the plantations were most successful in the province of Bolívar, in an area where other trees had been felled and burnt with the rest of the vegetation [2]. A type of *C. pubescens* with high quinine yield was cultivated in small plantings in the Andean foothills of central Ecuador [49]. In 1860, seeds and seedlings of this type were taken to India, Sri Lanka, and Guatemala [49, 54].

In its native and introduced range, *Cinchona* can be propagated through seeds and vegetative means but most commercial plantations are raised by seeds, and methods used were similar [12, 23, 39]. Typically, *Cinchona* seedlings are produced in raised seedbeds in soil mixed with leaf compost and manure. Seeds are thickly spread over the bed, for example, 2 g m^{-2}. The seeds are covered with a thin layer of soil under partial shade provided by roofing. The sown beds are kept moist and seeds germinate in 10–40 days, with a germination rate varying between 50 and 85 %. This way, 400 g of seeds can produce about 100,000 seedlings. After three months the seedlings have grown a pair of leaves and are planted out in rows with sufficient spacing (e.g. 5 × 5 cm). When seedlings are 10 cm tall, bearing three to four pairs of leaves, they are separated at 10–12 cm spacing. The partial shade can be removed after 3 months to expose the plants to the sun for the next four months. This way, it takes about 16 months to obtain seedlings of 20–25 cm in height, which are ready to be planted in the field at 1–2 m spacing. Trees are thinned after the third year for extracting the bark, leaving 50 % of the original number of trees at the end of the fifth year. In India, about 3000 *C. pubescens* individuals are planted per hectare, leaving space in between for the planting of shade trees, like *Crotalaria anagyroides* and *Tephrosia candida* which also serve as nitrogen fixers or for *Alnus nepalensis* and *Aleurites* spp., also as shade trees. In addition, about 100 kg each of nitrogen and phosphorus are applied per hectare as well as other micronutrients.

Greenhouse experiments in Puerto Rico revealed that *C. pubescens* grows best at temperatures ranging from 21 to 27 °C and that the total alkaloids and quinine content in roots and stems are also higher compared to cultivation at lower temperatures [67]. However, seedling survival is lower since leaves grow larger at these temperatures which apparently resulted in death of the weaker plants [67]. Seeds from India begin to lose their viability after six to eight weeks and lose it completely after one year [44]. Seeds in Galápagos also lost their viability after approximately one year [56].

Abb. 14: C. pubescens trees in the natural range: Botanical Garden of the Universidad National de Loia, Ecuador, 2160 masl (approx. height: 7 m)

Fig. 15: New shoots emerging from a cut Cinchona pubescens tree in Galápagos

In some countries like India, Sri Lanka, and Guatemala, *C. pubescens* is propagated using vegetative techniques, such as grafting, budding, and softwood cuttings, which are safer than propagation by seedlings [12, 39, 41]. The best wood for cuttings is the thin wood of the current year's growth [41]. The cuttings are taken just below the joint or point where a pair of leaves originated. They are then put out in thatched beds as already described for seedlings. They can also be grown in boxes about 5 cm deep, filled with a layer of vegetable mould mixed with sand. A layer of pure sand above the mould promotes drainage, since cuttings are apt to rot off at the level of the soil if not thoroughly drained. These cuttings form new roots in two to four months, according to season and temperature [41]. Even though *C. calisaya* yields more quinine, *C. pubescens* is often the predominant species in plantations because it is hardier, easier to propagate, and has a much wider range of growth conditions [41]. Therefore, it is used as a root stock for the grafting of *C. calisaya* (e.g. in Indonesia) because of its hardy and vigorously growing nature at lower elevations [12]. Hormonal treatments help to induce better rooting [39]. Nowadays, the propagation of *C. pubescens* is much easier. Twenty thousand shoots of *C. pubescens* can be obtained from the apical meristem of a plant by micropropagation within one year. However, this way the root development of the shoots is often inadequate so that the transfer of the shoots to the soil can be complicated [43].

Ecology

Habitat and climate requirements

Generally, in its natural range, *Cinchona* trees need warm climates with high precipitation and humidity almost all year round for optimal growth [2, 22]. In Ecuador, temperatures vary between 10 and 23 °C and *C. pubescens* often grows in steep gorges that are difficult to access and in disturbed habitats [2]. Soils are volcanic and rich in organic matter, nitrogen and phosphorus, but poor in potassium [2], are warm (16.3 °C on average), and slightly acid (pH 5.1 [22]). Trees also grow well in clay soils and in very rocky areas, where the roots are exposed to the air [2]. Soils around Loja in southern Ecuador, where several *Cinchona* species grow, mainly comprise decomposed micaceous schist and gneiss, covered by a layer of vegetable mould [41]. In Bolivia, cultivated *C. pubescens* trees grow best on the sides of valleys or ridges of the Andes at altitudes of about 900–1200 m. They will also grow up to 2400 m in altitude but then acquire a stunted growth form and will not yield much quinine [23].

Experimental investigations in Guatemala, India and Java showed that *Cinchona* grows best in well-drained soils with high organic matter, high nitrogen content, and low carbon/nitrogen ratio. These soils are also usually rich in citric-soluble phosphate, lime, and hydrolytic acidity and trees developed well in gentle as well as steep slopes with protection against erosion [12, 13, 41, 54]. In India, *C. pubescens* grows best at elevations between 460 and 2000 m asl, where it withstands both high humidity and dry conditions [12, 16]. As in its native range, *C. pubescens* grows better in recently cleared forests than in grasslands [41]. In Tahiti, *C. pubescens* has its growth optimum between 600 and 950 m elevation in secondary and primary rainforests [65] but was also found at up to 1400 m elevation in undisturbed cloud forest [51]. In São Tome and Príncipe and in Java it grows best at elevations of 650–1350 m and 1250–1950 m, respectively [16]. Optimal growing temperatures in India are 21–24 °C and should not go below 8 °C in winter and 30 °C in summer [12].

Competition

In Ecuador, *C. pubescens* does not usually occur as isolated individual trees nor as a forest but in small groups of trees, in "patches" [4, 22]. This was already the case in the area of Loja in 1737 and in other parts of the country, and was attributed to the cutting of large trees [25, 62]. *C. pubescens* is not a dominant tree species and has almost been brought to extinction through overexploitation during the 200 years up to World War II [5]. It is now considered endangered in its natural range in the south of Ecuador [26]. In contrast, in northern Peru, *C. pubescens* occurs as a dominant forest tree where it can reach a height of up to 30 m and a DBH of 90 cm [31].

In its introduced range, *C. pubescens* is much more competitive in its growth and has become invasive in some areas, meaning that it successfully reproduces and spreads without human intervention. This is especially the case in Galápagos, Hawaii, and Tahiti, where it outshades and reduces the cover of native plant species [19, 36, 37, 65]. Cultivation of *Cinchona* was initiated in Hawaii in 1868 and, by 1978, *C. pubescens* had naturalized [63]. In Galápagos, *C. pubescens* was introduced in the 1940s [28, 45] and had naturalized by 1972 [28]. In Tahiti, *C. pubescens* was introduced in 1938 [65] and has naturalized since the 1970s [50]. *C. pubescens* has also been reported to occur outside of plantations in Java and New Guinea [7], in Jamaica [58], Guatemala [49], and on St Helena [14].

Biological characteristics of *C. pubescens* in its introduced range that make it a good invader include its abundant seed production, e.g. in Hawaii and Galápagos. However, its light, wind-borne seeds do not seem to be dispersed very far from the parent tree. The maximum dispersal distance in Galápagos was 15 m [56] and in Hawaii it was reported that the species does not disperse further than 100 m from the parent tree [63]. The successful invasion of *C. pubescens* on both archipelagoes was a slow but continuous one. This is reflected in the long time that passed between the introduction of the species and the recognition that it had naturalized (over 100 years in Hawaii, and about 30 years in Galápagos [28, 63]). The youngest mature trees were observed in Galápagos, where 2-year-old seeding trees of 1.8 m height with a DBH of 1.5 cm produced fruit (H. JÄGER, pers. observ.). Another invasive characteristic of *C. pubescens* is the ability of the seeds to germinate in dense understorey vegetation as well as under a dense *C. pubescens* canopy, as in Hawaii and Galápagos [52, 63]. Last but not least, *C. pubescens* has a rapid vegetative reproduction by vigorous suckering from roots and stems [37, 46]. In addition, it demonstrates fast growth in its introduced range: about 1 m per year in Galápagos and 1–2 m elsewhere ([24], H. JÄGER, pers. observ.).

C. pubescens also may benefit from increased nutrient uptake due to its association with arbuscular mycorrhizal fungi, which are mainly lacking in native species in Galápagos [59].

Associations, communities

In Ecuador, *Cinchona* species tend to be associated with certain other tree species, like *Palicourea* spp., *Joosia pulcherrima*, *Hoffmania ecuatoriana*, *Hieronyma macrocarpa*, *Ocotea* spp., and *Weinmannia fagarioides* [3]. Old trunks of *C. pubescens* are generally covered with moss, liverwort, and lichen species [3], and this is also the case in Galápagos (mainly *Frullania* and *Omphalanthus* species, F. ZIEMMECK, pers. comm. 2007). In Peru at an elevation of about 2445 m, *C. pubescens* is mainly associated with various *Miconia* spp., *Clusia* spp., *Weinmannia pinnata*, *Hedyosmum scabrum*, *Chusquea scandens*, *Ilex* sp., and *Hesperomeles* sp. Below this elevation in the dwarf forest with short vegetation (1.5 m), *C. pubescens* is associated with other trees of the genera *Clusia*, *Befaria*, *Wemmannia*, and *Brunellia* [6].

Pathology

The databases of the Systematic Mycology and Microbiology Laboratory lists 27 fungi species as associated with *C. pubescens* but 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. [17]). The scab-causing pathogen *Elsinoe cinchonae* JENKINS was also recorded from *C. pubescens* from western Ecuador (H. C. EVANS, pers. comm. 2009). However, there is no evidence that these species are important economic pathogens [53].

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" [12, 13, 54]. These fungi penetrate the seedlings through their roots and cause sudden wilting and rotting of seedlings. In Java and India, plants were also attacked by the insects *Helopeltis* (tea mosquito) and *Pachypeltis* (leaf scorch) [12, 13]. *Cinchona* stem bark disease due to *Phytophthora cinnamomi* RANDS is a major disease in central African countries (Rwanda and the Democratic Republic of Congo) [12]. In Galápagos, secondary pathogens were isolated from *C. pubescens*, mainly *Fusarium* spp. and *Botryodiplodia theobromae* PAT. (H. C. EVANS, pers. comm. 2009).

Use

Because of its alkaloids, *Cinchona* is one of the most widely produced and traded medicinal plants [30], and the alkaloids extracted from *C. pubescens*, "red bark", and *C. calisaya*, "yellow bark", are commercially most important [7, 20]. Chemical components of interest extracted from the bark of the trunk (but also of twigs and roots) are quinine, quinidine, cinchonidine, and cinchonine [12, 20]. The most important is quinine, which, in the form of quinine salts, like sulfate, bisulfate, hydrochloride, and dihydrochloride, was used for the prevention and treatment of malaria [12] before the chemical synthesis of quinine was achieved by the American chemists WOODWARD and DOERING in 1944 [68].

There are three common ways of harvesting *Cinchona* bark: uprooting, coppicing, and mossing. In the first case, the complete tree is uprooted and the bark stripped off the trunk [39]. When coppicing a tree, the trunk is cut close to the ground, thereby inducing the production of basal sprouts to produce a second crop of bark [55]. However, the trees recover slowly from this treatment and the bark does not contain as much alkaloid as first-stem bark [23]. Since it was observed that the best *Cinchona* was always covered with moss, in "mossing" the bark was stripped off the trunk and the bare trunk subsequently covered with moss. This system was practiced in Java and Sri Lanka, and induced the cambium to produce a second bark which contained up to three times higher alkaloid content than the first [23, 60]. A fourth approach for the bark harvest was used in Loja (Ecuador) where people stripped the bark from standing tall trees as far as they could reach. Then they made steps by tying sticks to the tree with ropes so they could harvest the bark further up until they reached the top of the tree [25]. Apparently, this practice was limited and felling the *Cinchona* trees was much more common, leading to the near-extinction of *Cinchona* species (especially *C. pubescens*) in that area [4, 32].

For commercial distribution, the stems and roots are cut into pieces, the bark is then separated, dried, graded, packed, and traded [39]. In Bolivia, the bark is placed in paved yards and generally dries in four days to three weeks, depending on the weather conditions [23]. As early as 1737 it was noted that the *Cinchona* with the "red bark" from Loja (probably *C. pubescens*) has a much better curative effect when used fresh and green, and turns worthless when dry and long kept [25].

The wood of *Cinchona* also contains alkaloids and therefore was the preferred building material for houses in Southern Ecuador, since it was one of the more termite-resistant woods [9]. Even though the wood is of inferior quality in Galápagos, it is now increasingly used for construction, since alternative wood is getting scarce due to overexploitation or governmental regulations (H. JÄGER, pers. observ.).

Since World War II, the main part of the quinine yield has gone towards the production of pharmaceutical compounds, like antipyretic drugs against colds, flu, and rheumatism. The remaining part in the form of quinine hydrochloride and quinine sulfate is used in the beverage industry, mainly as a bitter flavor in tonic water and bitter lemon [12, 20] and might still have some prophylactic value against malaria. Quinidine is used as a cardiac depressant and its sulfate form is used for the treatment of cardiac arrhythmia [12]. Today, between 400–700 tons of alkaloids are obtained from 8000–10,000 tons of bark produced annually [20, 35]. In 2000, 1 kg of quinine cost ca. US $ 500 and quinidine ca. US $ 1500 because of its naturally lower occurrence [20].

Miscellaneous

Control

C. pubescens has long been recognized as a potential risk to native vegetation in its introduced range, especially in Hawaii, Galápagos, and Tahiti. In the Galápagos National Park, several control methods to combat *C. pubescens* have been implemented. Manual methods include felling and uprooting of trees, as well as hand-pulling of smaller plants, but trees resprout from cut stumps [8, 46]. Chemical control methods consist of applying herbicides by a range of means: hack and squirt, basal bark, cut stump, girdle and squirt, branch filling, tree injections, and foliar spray [8]. However, most of these methods were ineffective in the long run. Eventually, a hack and squirt technique was developed in which a mixture of picloram and metsulfuron was applied to connecting machete cuts around the circumference of tree trunks, which killed 73–100 % of the trees. Smaller shoots and saplings were pulled out by hand [8]. This method is now successfully applied for *C. pubescens* control by the Galápagos National Park Service on a small scale, as well as the uprooting of trees in conservation priority areas [38]. Control of *C. pubescens* would be difficult in Hawaii (mainly Maui), since it primarily grows in steep gulches and thick understorey vegetation. However, control of small populations in spots of native vegetation could prevent further spread and help to slow down the degradation of the remaining native forest in the area [63].

Pathogens attacking *C. pubescens* in its native range in Ecuador have been isolated but it remains to be seen whether these might be potential biological control agents (H. C. Evans, pers. comm. 2009).

History of discovery and cultivation of *Cinchona*

The early history of the use of quinine is obscure and the question of whether the indigenous people of South America knew about its curative properties remains controversial. Some authors argue that quinine was used to treat different fevers (not malaria) in Peru and Ecuador before the arrival of the Spaniards [32, 47] and some argue that the people did not know about its fever-reducing characteristics [33, 62]. However, GRAY et al. [25] reports that it was the current opinion in Loja (Ecuador) that the qualities and uses of *Cinchona* bark were known by the indigenous people before the arrival of the Spaniards and that it was applied by them to cure "intermittent fevers", which were "… frequent over all that wet unhealthy country" [25].

The way quinine made its way to Europe is another mystery. The most frequently cited version is that the COUNTESS OF CHINCHÓN returned to Spain in 1642 and brought with her a stock of *Cinchona* bark to cure malaria there [47]. This was reason enough for LINNAEUS to name the genus *Cinchona* in her honor in 1742, erroneously leaving out an "h" when doing so [48]. However, this version is not true since the first wife of the Viceroy died before she left Spain for Peru and his second wife died in Colombia before she could return to Spain [27]. In addition, the official diary of the Viceroy, kept by his secretary, was found in 1930 and revealed that his second wife had never fallen ill with a fever [27].

Even the point of time when *Cinchona* was brought to Europe is not clear, since the bark of the Peruvian balsam tree (*Myroxylon peruiferum*) had been shipped to Rome at the beginning of the 17th century under the name "quina-quina" (Quechua word meaning "bark of barks") [40] and the actual *Cinchona* bark was only exported to Europe from 1631 [57] or the mid-1600s [40] onwards. *Cinchona* was superior to Peruvian balsam in its feverreducing qualities [32, 40]. The Augustinian and Jesuits were apparently really the first to bring *Cinchona* bark to Europe and distribute it as a remedy against malaria (hence the name "Jesuit's bark" [40]). In 1677, *Cinchona* bark entered the London Pharmakopoeia as "Cortex Peruvianus" (Peruvian bark) [40].

Cinchona was the first effective treatment for malaria, and in 1820 PELLETIER and CAVENTOU isolated quinine and cinchonine from the *Cinchona* bark, of which quinine was the main antimalarial ingredient [21]. After this successful isolation, quinine extract quickly replaced the untreated *Cinchona* preparations in the treatment of malaria. Supplies of quinine were limited and the need was great. Malaria was affecting millions of people in the Asiatic tropics and in Africa, and the imperialistic activities of Europeans in these areas required high amounts of quinine, which prompted the cultivation of *Cinchona* [21, 54].

It is notable that 200 years passed between the discovery of the genus *Cinchona* and its cultivation. The reasons are likely the rather difficult cultivation of the tree and the initially abundant supplies of wild bark, sufficient to meet demands in Europe and America [54]. Several investigators visiting the natural sources of *Cinchona* in the Andes had pointed out that the trees were in danger of extermination as a consequence of overexploitation [23, 25, 54]. VON HUMBOLDT reported that 25,000 trees were cut annually in the Andes in 1795 [33]. The Dutch were the first in reacting to the increase in the demand for the *Cinchona* bark by sending the German botanist HASSKARL to the Andean region in 1852 to obtain *Cinchona* seeds [55]. The British followed shortly after by sending SPRUCE into the forest of the western slopes of Mount Chimborazo in Ecuador to collect *Cinchona* seeds and plants (also of *C. pubescens*) to start a plantation in India in 1860 [62]. MARKHAM also investigated the *Cinchona*-producing areas in South America and collected plants and seeds for these plantations [47]. In 1865, LEDGER obtained seeds from a superior *Cinchona* strain (*C. calisaya*), enabling the Dutch to assume world dominance in quinine production from the 1890s onwards through their plantations in Java [54, 55]. Before World War II, about 90 % of the world supply of *Cinchona* bark was produced in Java [12]. When Java was occupied by the Japanese in 1942, natural quinine became very scarce, which led to the development of a synthetic production of quinine alkaloid in 1944 [68].

Significance of Cinchona today

The need for effective antimalarial drugs has persisted over the nearly two centuries since quinine was first isolated [21]. The evolution of strains of the malaria parasites resistant to the synthetic drugs (mainly chloroquine), and the consequent rise in the malaria incidence in Asia and Africa, have revitalized interest in quinine and in the antimalarial properties of the other alkaloids of *Cinchona* [21, 35]. Other natural antimalarials in the bark's extract, such as quinidine, appear to potentiate the effects of quinine [18]. This, coupled with the increasing use of quinidine as an antiarrhythmic compound, has increased the demand for *Cinchona* bark [35].

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Fig. 16: C. pubescens trees in the introduced range: highlands of Santa Cruz Island, Galápagos (670 masl)

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