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Distribution and environment-rhodomyrtone of *Rhodomyrtus tomentosa* in Peninsular Thailand

NUTCHANART KONGCHUAY[1], JUTARUT IEWKITTAYAKORN[2,3], AUNKAMOL KUMNGEN[3], SUPAYANG P. VORAVUTHIKUNCHAI[4], SARA BUMRUNGSRI[2,♥]

[1]Division of Physical Science, Faculty of Science, Prince of Songkla University. 15 Kanchanawanit Rd., Hat Yai 90112, Songkhla, Thailand
[2]Division of Biological Science, Faculty of Science, Prince of Songkla University. 15 Kanchanawanit Rd., Hat Yai 90112, Songkhla, Thailand. Tel.: +66-74-288022, Fax.: +66-74-558844, ♥email: sara.b@psu.ac.th
[3]Center for Genomics and Bioinformatics Research, Faculty of Science, Prince of Songkla University. 15 Kanchanawanit Rd., Hat Yai 90112, Songkhla, Thailand
[4]Center of Antimicrobial Biomaterial Innovation-Southeast Asia, Prince of Songkla University. 15 Kanchanawanit Rd., Hat Yai 90112, Songkhla, Thailand

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Abstract. *Kongchuay N, Iewkittayakorn J, Kumngen A, Voravuthikunchai SP, Bumrungsri S. 2026. Distribution and environment-rhodomyrtone relationship of* Rhodomyrtus tomentosa *in Peninsular Thailand. Biodiversitas 27 (3): d270312. https://doi.org/10.13057/biodiv/d270312*. *Rhodomyrtus tomentosa* is a medicinal plant that yields the antibiotic compound rhodomyrtone. It has been depleted due to changes in land use, therefore, the ecological requirements of the species in its natural habitats need to be investigated to advance its commercial cultivation. This study aimed to explore environmental and soil physicochemical factors affecting the rhodomyrtone content present in *R. tomentosa* leaves. Soil texture and soil chemical properties were examined. Leaves were extracted and rhodomyrtone content was quantified. *R. tomentosa* was found in 54 sites in peninsular Thailand and mostly found in open areas, in acidic soil (pH 4.31-6.36) at low elevation (4-129.5 m asl). The results showed that the species is found in poor soil with very low nitrogen, phosphorus, and potassium contents. *R. tomentosa* predominantly grows in sandy soil containing fine to coarse sand (125-500 μm). No significant correlation was observed between rhodomyrtone content and soil pH, % organic matter, N, P, or K. In contrast, rhodomyrtone content positively correlates with percent shade cover. Further experimental study is needed to confirm this observation. For commercial cultivation, this shrub should be planted in lowland, sandy, nutrient-poor soil of low pH, and under light shade to promote rhodomyrtone production.

Keywords: Low elevation, medicinal plant, *Rhodomyrtus tomentosa*, sand bar, sandy soil

INTRODUCTION

Rhodomyrtus tomentosa (Aiton) Hassk. is a shrub in the family Myrtaceae that exhibits a broad spectrum of pharmacological effects. Traditionally, it has been used to treat colic diarrhea, gynecopathy, heartburn, abscesses, wounds, and as a painkiller (Isnaini et al. 2019). While the fruit is commonly eaten, the roots and leaves are locally utilized for the treatment of diarrhea. It is widely distributed in China, Taiwan, the Philippines, Malaysia, Indonesia, and Vietnam (*Rhodomyrtus tomentosa* var. *tomentosa*), India, and Sri Lanka (*Rhodomyrtus tomentosa* var. *parviflora*). It is reported to have invaded French Polynesia, Hawaii and Florida in the USA (Xie et al. 2021).

The species typically grows to a height of 2-4 m (Rani et al. 2024). It inhabits open areas, often degraded sandy sites, along riverbanks, and seashores (Latiff 1992). In China, it is also found in moist and wet forests, shrublands, wetlands, bogs, and ponds (Yang et al. 2010; Liu et al. 2013). It is not soil-specific (Bailey and Bailey 1976), but tolerates salinity (Menninger 1964) and prefers acidic and infertile soils (Xie et al. 2021; Frohlich 2022). Its growth is limited when light transmission through the canopy falls below 30% (Hai et al. 1997; Frohlich 2022). *R. tomentosa* is one of the principal shrubs found in young plantations in southern China and contributes to carbon storage in these ecosystems (Chen et al. 2017). It is bee-pollinated and the primary pollinators are *Amegilla florea* and the carpenter bee, *Xylocopa nasalis* (Wei et al. 2009). Its seeds are dispersed by birds and ants. In harsh environments, *R. tomentosa* acts as a nurse plant, providing optimum conditions for the establishment of native pioneer species (Yang et al. 2010; Liu et al. 2013).

This highly resilient medicinal shrub faces increasing threats from habitat loss and land use changes that have caused its populations to decline. In Thailand, this species found in southern and southeastern region. Detcharoen et al. (2023) revealed low genetic differentiation across populations in southern Thailand. Despite its resilience**,** this shrub has been largely eradicated as it grows naturally on infertile land, which is classified as “not being utilized as it should” in the latest land tax reports. Since landowners are taxed highly for areas in this classification, these lands have mostly been cleared and converted to farmland. Currently, commercial cultivation of this plant does not exist in Thailand.

The plant has become valued for its bioactive compound, rhodomyrtone. *R. tomentosa* leaf extract and fruit phenolics

exhibit potent antimicrobial and antioxidant properties (Divya Priya and Martin 2025). Rhodomyrtone, the principal compound of *R. tomentosa*, has been proposed as a novel antimicrobial drug with a unique mode of action. This compound is highly active against various bacteria (Limsuwan et al. 2009; Saising and Voravuthikunchai 2012; Chorachoo et al. 2013). Moreover, *R. tomentosa* has shown potential as a new anticancer compound (Situmorang et al. 2024). The excellent biological properties of rhodomyrtone have resulted in the adoption of *R. tomentosa* extracts by the cosmetic, pharmaceutical, and food industries, which has inevitably spurred the demand for these extracts (Nhan et al. 2019).

Characterizing the specific environmental requirements of *R. tomentosa* in its natural range is a prerequisite for optimizing commercial planting protocols. Such information is also vital for the restoration of its lost populations. Although it is still not known if soil or other environmental factors influence rhodomyrtone content, it has been reported that plants were stimulated to produce phenolic compounds by high light intensity (Arena et al. 2017). The present study aimed to determine soil physicochemical properties and other habitat characteristics of existing populations in peninsular Thailand, and investigate environmental factors related to rhodomyrtone content in *R. tomentosa* leaf. It is hypothesized that the rhodomyrtone content in *R. tomentosa* leaves is influenced by environmental factors, particularly soil properties (pH, N, P, K, soil organic matter) and canopy cover.

MATERIALS AND METHODS

Survey of natural populations and sample collection

Since *R. tomentosa* usually grows in low-lying land, purposive sampling was employed. All subdistricts in southern Thailand that are mostly less than 300 m asl were identified. The species groves were located by interviewing local volunteers of the Land Development Department, especially in areas along ancient beaches on both coasts of peninsular Thailand. A total of 54 study sites across peninsular Thailand are listed (Figure 1, Table 1). When natural groves of this plant were known to be present, voucher specimens of *R. tomentosa* were collected. 60-80 mature leaves, from 3 to 11 plants within the same grove were collected. For each grove, 2-3 subsamples taken at 15 cm depth, which is the topsoil layer where most nutrient uptake occurs, were composited to form one representative sample per site. The level of openness above the shrubs was estimated with a hemispherical lens attached to a mobile phone camera positioned vertically over the shrub at two or three locations per site. The percentage of canopy cover was determined by analyzing digital photographs with the Gap Light Analysis Mobile Application (Lubomir Tichy, Department of Botany and Zoology Masaryk University Brno, Czech Republic).

Procedures

Soil and leaf samples were transported to the Faculty of Science, Prince of Songkla University, Thailand. Soil samples were subjected to physicochemical analysis (chemical properties and texture), whereas leaf samples were analyzed for rhodomyrtone content.

Soil chemical properties

Soil samples were analyzed for pH, N, P, K, organic matter, and electrical conductivity in the central laboratory, Science Faculty, Prince of Songkla University. All laboratory analyses were conducted following standard AOAC (2023) procedures. Soil pH was measured in a 1:1 soil-water suspension using a digital pH meter. Total N (g/kg) and soil organic matter (g/kg) were determined by CN Analyzer, while total P (g/kg) was determined by spectrophotometry. Total K (g/kg) concentration was determined using inductively coupled plasma optical emission spectrometry (ICP-OES) after acid digestion of the samples. The emitted light intensity at the characteristic wavelength of K was measured and quantified against certified calibration standards. Electrical conductivity (mS/m) was analyzed with a TDS meter.

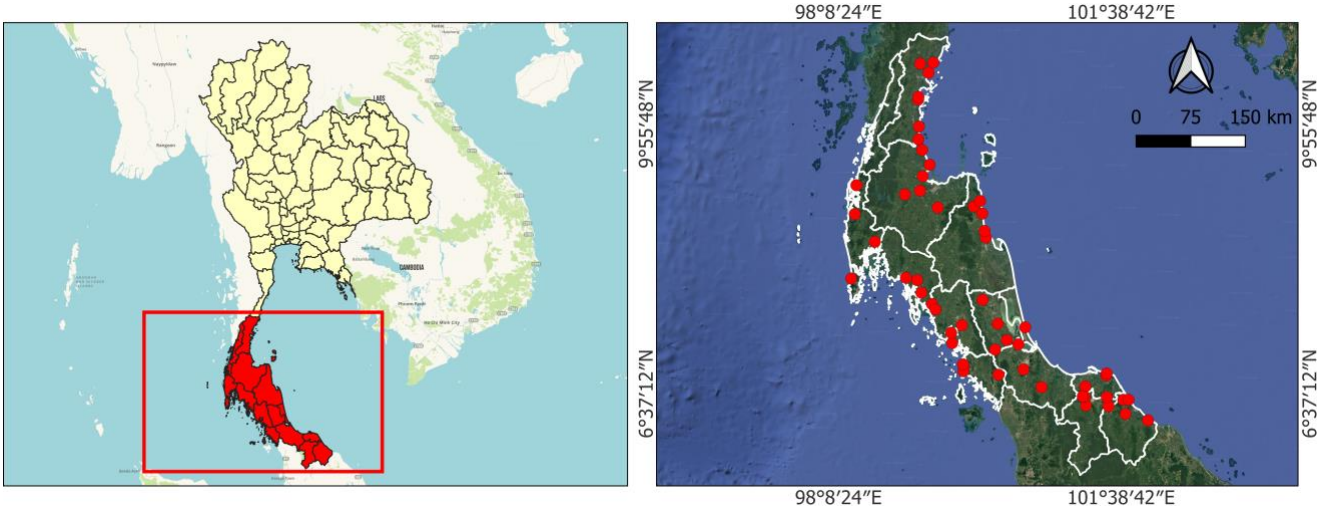

Figure 1. Location of collecting sites of *Rhodomyrtus tomentosa* in Peninsular Thailand

Table 1. Collecting sites of *Rhodomyrtus tomentosa* in Peninsular Thailand

Code	Subdistrict	District	Province	Latitude (N)	Longitude (E)	Elevation (m asl)
CHP-01	Suanthaeng	Lamae	Chumporn	9.74209	99.13034	36
CHP-02	Thahin	Sawi	Chumporn	10.22547	99.12770	164
CHP-03	Pakprag	Sawi	Chumporn	10.25948	99.13177	48
CHP-04	Nacha-ung	Muang	Chumporn	10.55229	99.25802	83
CHP-05	Thasae	Thasae	Chumporn	10.66415	99.15440	72
CHP-06	Bangson	Pathew	Chumporn	10.67712	99.31654	17
CHP-07	Bangmaphaew	Lungsuan	Chumporn	9.89717	99.13782	71
SRT-01	Thachana	Thachana	Suratthani	9.60898	99.17858	45
SRT-02	Thakob	Chaiya	Suratthani	9.43034	99.27117	23
SRT-03	Khaothan	Thachang	Suratthani	9.28917	99.18554	21
SRT-04	Thakanon	Kiriratnikom	Suratthani	9.06649	98.96302	102
SRT-05	Nongsai	Phunphin	Suratthani	9.11164	99.15202	24
SRT-06	Thungtao	Nasarn	Suratthani	8.90611	99.37111	40
PNG-01	Bangsai	Thakuapa	Phangnga	8.82670	98.34251	43
PNG-02	Maemangkhao	Kuraburi	Phangnga	9.17965	98.36263	48
PNG-03	Borsaen	Thabpud	Phangnga	8.48687	98.59118	57
PKT-01	Cherngthalae	Talang	Phuket	8.03586	98.29765	40
KRB-01	Saikhao	Klongthom	Krabi	7.72217	99.30037	65
KRB-02	Pela	Klongthom	Krabi	8.01635	99.11572	118
KRB-03	klongkamao	Nuaklong	Krabi	8.04490	98.97780	121
KRB-04	Huaynamkhao	Klongthom	Krabi	7.86206	99.16901	41
NST-01	Pakphum	Muang	Nakornsrithammarat	8.53958	99.96834	41
NST-02	Thasala	Thasala	Nakornsrithammarat	8.61936	99.95199	22
NST-03	Klai	thasala	Nakornsrithammarat	8.83247	99.92405	44
NST-04	Chalong	Sichon	Nakornsrithammarat	8.91965	99.81751	94
NST-05	Thungprang	Sichon	Nakornsrithammarat	8.98706	99.89604	34
TRG-01	Thungkhai	Yantakhao	Trang	7.46294	99.67112	62
TRG-02	Hatsamran	Hatsamran	Trang	7.24331	99.55039	14
TRG-03	Kanthang	Kanthang	Trang	7.36824	99.53774	90
TRG-04	Khaomaikaew	Sikao	Trang	7.65579	99.34301	71
PTL-01	Thungnari	Phabon	Phattalung	7.16286	100.08289	425
PTL-02	Hanthao	Pakpayun	Phattalung	7.27910	100.22760	44
PTL-03	Kuankanun	Khaochaison	Phattalung	7.47968	100.11621	45
PTL-04	Chamuang	Kuankanun	Phattalung	7.77400	99.92796	106
SKL-01	Khuanso	Khaunniang	Songkhla	7.22683	100.37168	32
SKL-02	Plaknoo	Nathawee	Songkhla	6.70031	100.65953	142
SKL-03	Thunglan	Klonghoykong	Songkhla	6.91768	100.43613	49
SKL-04	Bodarn	Sathingphra	Songkhla	7.43689	100.45583	27
SAT-01	Laemson	Langu	Satul	6.94617	99.69568	18
SAT-02	Paknum	Langu	Satul	6.89675	99.68997	20
SAT-03	Khonkhan	Thungwa	Satul	6.98042	99.68520	37
SAT-04	Thungnui	Kuankalong	Satul	6.85300	100.12579	174
PAT-01	Parai	Maelan	Pattani	6.70799	101.20161	48
PAT-02	Yaring	Yaring	Pattani	6.84325	101.46213	28
PAT-03	Panarae	Panarae	Pattani	6.86956	101.46634	25
NAT-01	Baraetai	Bajua	Narathiwat	6.54470	101.67356	30
NAT-02	Yingor	Yingor	Narathiwat	6.37078	101.70025	74
NAT-03	Khokkian	Muang	Narathiwat	6.54547	101.73737	32
NAT-04	Praiwan	Takbai	Narathiwat	6.29166	101.97814	15
YAL-01	Natham	Muang	Yala	6.47575	101.20987	152
YAL-02	Talohalor	Ramun	Yala	6.46652	101.49007	125
YAL-03	Thathong	Ramun	Yala	6.57813	101.46908	63
YAL-04	Lummai	Muang	Yala	6.57963	101.19449	119
YAL-05	LumPhraya	Muang	Yala	6.58734	101.17057	134

Soil texture analysis

Soil texture was determined from grain sizes. Soil samples of 750-1500 g were oven-dried at 50°C for 3 days. Dried soil samples were sieved with shaking. Particles were separated into fractions of 2000, 1000, 500, 250, 125, 63, and smaller than 63 µm. The percentage by weight of each fraction was then determined (Gee and Or 2002). The Wentworth grain size classification was applied to classify soil fractions as granules (more than 2,000 µm) very coarse sand (1,000-2,000 µm), coarse sand (500-1,000 µm), medium sand (250-500 µm), fine sand (125-250 µm), very fine sand (63-125 µm), and silt (<63 µm) (Wentworth 1922). Soil

texture was analyzed at the Zoology Laboratory of the Biological Science Division, Prince of Songkla University, Hat Yai.

Leaf extraction and rhodomyrtone quantification

Rhodomyrtus tomentosa leaves were extracted following the method of Limsuwan et al. (2012) with slight modifications to improve extraction efficiency and reproducibility. Fresh leaves were washed thoroughly with distilled water, oven-dried at 60°C until a constant weight was obtained, and ground into a fine powder using an electric grinder. Triplicate biological replicates (n = 3) were prepared for each treatment. Leaves from multiple plants were composited into one bulk sample per site and then split into 3 replicates. Approximately 20 g of powdered leaves were soaked in 95% ethanol (RCI Labscan, Thailand) at a leaf-solvent ratio of 1:10 (w/v) and incubated under dark conditions at room temperature (28±2°C) for 7 days with intermittent shaking at 150 rpm. The extracts were filtered through Whatman No. 1 filter paper, and the filtrates were concentrated under reduced pressure using a rotary vacuum evaporator (Heidolph, Germany) at 45°C. The resulting crude extracts were further dried under vacuum to constant weight. The dried extracts were dissolved in dimethyl sulfoxide (DMSO) (Merck, Germany) to obtain a stock solution of 10 mg/mL, which was subsequently diluted with methanol for HPLC analysis.

The quantitative determination of rhodomyrtone was performed using high-performance liquid chromatography (HPLC) (Agilent 1100 Series, USA), facilitated with a quaternary pump, autosampler, column oven, and UV-Vis detector. Separation was performed using a Zorbax Eclipse XDB-C18 reversed-phase column (4.6 × 250 mm, 5 µm particle size) (Agilent Technologies, USA) maintained at 35°C. The mobile phase consisted of acetonitrile and 0.1% (v/v) phosphoric acid in water at a ratio of 70:30 (v/v) with a flow rate of 1.2 mL/min. The injection volume was 20 µL, and detection was carried out at a wavelength of 254 nm. Each sample was analyzed in triplicate injections (technical replicates). The column was equilibrated for 6 min before each run and preconditioned with the mobile phase for at least 3 h prior to analysis to ensure stability. Quantification was performed using rhodomyrtone standard (≥95% purity) (Sigma-Aldrich, USA) as an external standard. A calibration curve was generated by analyzing serial dilutions of the standard solution in methanol (0.5-50 µg/mL). The calibration curve exhibited excellent linearity with a regression coefficient ($R^2 = 0.9992$). The concentration of rhodomyrtone in each extract was calculated based on the peak area of the standard curve. All values were reported as means ± standard deviation (SD) from three independent biological replicates.

Data analysis

Descriptive statistics (mean, SD, and range) were used to summarize environmental and soil properties. Rhodomyrtone quantity was tested for normality and categorized into three groups based on the 95% confidence interval of the mean. Relationships between rhodomyrtone quantity, environmental factors (elevation, percent cover), and soil properties (pH, nutrients, soil organic matter) were evaluated with correlation coefficients. Pearson correlation (two-tailed test) was used when data were normally distributed, while Spearman correlation was applied when it was not normally distributed. Normality was assessed with the Shapiro-Wilk test. Statistical analyses were performed using R software (version 4.2.0) at a significance level of 0.05.

RESULTS AND DISCUSSION

Habitat of *Rhodomyrtus tomentosa*

Fifty-four locations in southern Thailand with natural groves of *R. tomentosa* were identified (Figure 2). Based on the field survey, the habitats of *R. tomentosa* could be divided into three types: The first type comprised sandy areas close to the coast in Chumphon (CHP4), Pattani (PAT2), and Narathiwat (NAT3, 4). In these areas, only two or three other plant species were present, exposing *R. tomentosa* to direct sunlight due to the sparse canopy cover. The soil in these areas was primarily sandy, and the terrain was approximately 4 m above sea level; the second type comprised private and public flat land in degraded woodland strips near riverbanks, such as in Chumphon (CHP1, 5, 6), Krabi (KRB2), Trang (TRG1), and Phang Nga (PNG1, 2, 3). These sites supported top canopy species, such as *Melaleuca quinquenervia* and *Eucalyptus* sp., which provided some shade for *R. tomentosa*. The elevation of these areas was also around 4 m above sea level; the third type was private land used for growing plants commercially. These areas were in Krabi (KRB4), Pattani (PAT1, 3), and Narathiwat (NAT1). The land in these areas was similar to the land in the second habitat type; however, it was used to grow oil palm and rubber tree, which are the two main economic plants in southern Thailand. *R. tomentosa* plants were interspersed among these trees, but in small numbers. Most study sites were below 100 m in elevation (68.79±64.61 m msl., range 14-425 m asl.). *R. tomentosa* was mostly found in open areas (percent cover 14.72±12.6%, range 0.82-44.3%, n= 53).

Soil chemical properties and texture

The soil was mostly acidic (5.12±0.45), with a pH range from 4.31 to 6.36. *R. tomentosa* was mostly found growing in poor soil with very low nitrogen (0.76±0.3 g/kg, range 0.13-1.52 g/kg), phosphorus (0.07±0.11 g/kg, range 0.01-0.73 g/kg), and potassium contents (0.09±0.11 g/kg, range 0.01-0.41 g/kg). Soil organic matter was within the normal range in these areas (20.18±6.91g/kg, range 7.20-34.20 g/kg). The electrical conductivity of soil samples was low (2.0±1.3 mS/m, range 0.5-7.1 mS/m) (Table 2).

Most of the natural groves were found in sandy soil. Based on the Wentworth (1922) grain size classification, soil samples predominantly comprised largely similar proportions of fine sand (24.21%), medium sand (250 µm-grain size, 24.87%), and coarse sand (500 µm grain size, 17.59%), with minor proportions of granules (12.49%), very coarse sand (11.11%) and very fine sand (7.21%), with hardly any silt (<63 µm, 2.46%) (Table 3).

Table 2. Environmental characteristics and soil physiochemical properties of natural groves of *Rhodomyrtus tomentosa* in Peninsular Thailand (n = 54 sites)

	Elevation (m asl.)	Percent cover (%)	pH	Organic matter (g kg^{-1})	Electrical conductivity (mS/m)	Nutrient (g kg^{-1})		
						Total N	Total P	Total K
Mean	68.79	14.74	5.12	20.18	2.0	0.76	0.07	0.09
SD	64.61	12.6	0.45	6.91	1.3	0.30	0.11	0.10
Range	14-425	0.82-44.3	4.31-6.36	7.20-34.2	0.5-7.1	0.13-1.52	0.01-0.73	0.01-0.41

Table 3. Grain size distribution in soil samples collected from 54 natural groves of *Rhodomyrtus tomentosa*

Grain size class	Granules	Very coarse sand	Coarse sand	Medium sand	Fine sand	Very fine sand	Silt
Average percentage	12.49	11.11	17.59	24.87	24.21	7.56	2.46
SD	15.94	8.14	15.26	16.83	18.44	7.21	2.29

Table 4. Correlation between rhodomyrtone concentration and various soil and environmental variables

Variables	Correlation coefficient (r)	p-value
pH	0.06	0.70
Total N	-0.01	0.97
Total P	-0.18	0.47
Total K	-0.12	0.47
Soil organic matter	-0.13	0.44
Percent cover	0.46	< 0.005*

Note: *significant

Rhodomyrtone quantity

Rhodomyrtone contents were quantified in *R. tomentosa* from 44 sites in Peninsular Thailand (Figure 2). It was found that the rhodomyrtone content was normally distributed, with an average of 3.358 mg/ml and a standard deviation of 1.508 (95% CI of the mean, 2.894 to 3.822). Based on the 95% CI of the mean rhodomyrtone quantity, the study area can be classified into three groups, i.e., the lower bound (<2.894 mg/ml), which covered 21 sites (49%), the 95% CI of the mean (2.894-3.822 mg/ml), which covered 8 sites (19%), and the upper bound (>3.822 mg/ml), which covered 14 sites (32%) (Figure 2). This grouping was used only for mapping, not for statistical comparison.

The relationship between rhodomyrtone concentration and various soil and environmental variables

There was no significant relationship between rhodomyrtone content and any soil physicochemical property, including pH, total N, total P, total K, and soil organic matter (p>0.05). In contrast, the amount of rhodomyrtone was positively correlated with percent cover (r = 0.46, p<0.005)—the higher the percent cover, the higher the content of rhodomyrtone (Table 4). However, the degree of correlation was moderate.

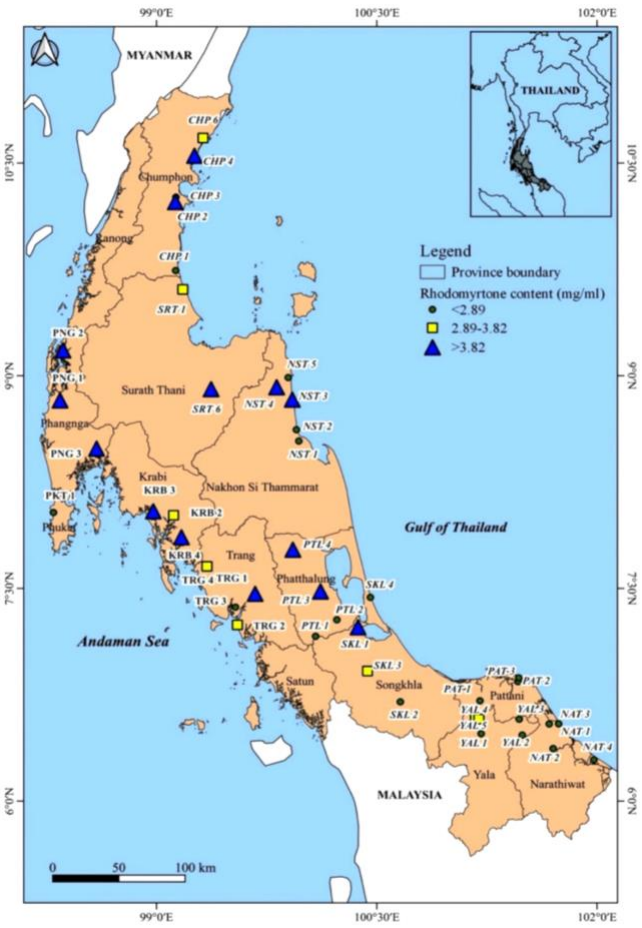

Figure 2. Distribution of *R. tomentosa* in Peninsular Thailand (44 locations). Triangles, circles and squares represent different rhodomyrtone leaf contents which were classified into three groups: the lower bound (<2.89 mg/ml, circle), covering 21 sites (49%), the 95% CI of the mean (2.89 to 3.82 mg/mL, square), covering 8 sites (19%), and the upper bound (>3.82 mg/mL, triangle), covering 14 sites (32%). See details of rhodomyrtone grouping in Rhodomyrtone quantity (below). Rhodomyrtone contents were not quantified in *R. tomentosa* plants from 10 of 54 sites

Discussion

The current study identified three distinct habitat types where this species persists, each presenting different ecological conditions that influence its growth and survival. The first habitat type, sandy coastal areas, represents a challenging environment for plant survival due to poor soil fertility and high exposure to direct sunlight. Despite these harsh conditions, *R. tomentosa* thrives in these areas, suggesting its adaptability to nutrient-deficient sandy soils. Similar resilience has been observed in some other species within coastal ecosystems (Frohlich 2022; Athulya et al. 2023). However, the lack of canopy cover may increase vulnerability to extreme weather conditions and salt spray, potentially affecting seedling recruitment and long-term population stability (Remelgado and Meyer 2023). The second habitat type, degraded woodland strips near riverbanks, provides a more favorable microenvironment due to partial shading from taller canopy species, such as *M. quinquenervia* and *Eucalyptus camaldulensis*. The accumulation of organic matter from fallen leaves enriches soil, which may contribute to improved growth conditions (Bhardwaj et al. 2022). Other shade-tolerant species suggest that partial shading can reduce photodamage while enhancing photosynthetic efficiency (Li et al. 2014; Liu et al. 2019). This proposition supports the idea that moderate shade may be beneficial for *R. tomentosa*, particularly in degraded landscapes where competition from taller species is less intense. The third habitat type, private land used to cultivate the oil palm and rubber tree, provides evidence that *R. tomentosa* can coexist within agroecosystems. The application of fertilizers in these areas may contribute to soil enrichment, yet the presence of only small numbers of *R. tomentosa* suggests that intensive agricultural management could limit its regeneration. The transition from natural ecosystems to monoculture plantations is a common cause of biodiversity loss in tropical regions (Zhu et al. 2023), and conservation efforts should consider integrating *R. tomentosa* into sustainable land-use practices, such as agroforestry systems that balance economic and ecological benefits.

The description of a natural grove of *R. tomentosa* in Thailand corresponds to previous descriptions in other countries. Similar to populations of *R. tomentosa* in China (Wei et al. 2009; Yang et al. 2010), the main populations found in the current study were found in flat areas below 100 m asl. The species is commonly found in sandy areas adjacent to the sea. The soil samples taken from these groves comprised very small soil grains and were of low pH. These characteristics implied that the shrub had established itself on former sandbars, which are common along the flat coastal zone of southern Thailand. Sandbars in this region are formed by the deposition of sand during sedimentation. The inland groves were often located along small tributaries and streams which usually flooded in heavy seasonal rains. Here, natural populations were often found in bogs with acidic soil. Although this species is not soil-specific (Bailey and Bailey 1976), it is very rarely found in open fertile soil at the edge of upland forest. The low pH observed in these habitats plays a critical role in nutrient dynamics. In these acidic conditions, the solubility of essential macronutrients, particularly phosphorus, is often limited as it tends to fix with aluminum or iron (Xie et al. 2021). The ability of *R. tomentosa* to thrive in such environments suggests a high physiological tolerance for acid-induced stresses, such as Al toxicity or Mo deficiency, which typically inhibit the growth of less resilient species. This acid-tolerance functions as an environmental filter, allowing *R. tomentosa* to dominate habitat like former sandbars and coastal area. In this sandy coastal area, soil organic matter is generally low, leading to poor cation exchange capacity and rapid nutrient leaching. Conversely, in the inland bogs and riparian sites where *R. tomentosa* was also found (Yang et al. 2010), organic matter may accumulate due to anaerobic conditions caused by seasonal flooding. However, the high acidity in these bogs often slows the decomposition rate, resulting in high organic matter that is unavailable. The presence of *R. tomentosa* in both low organic matter sandy soils and high organic matter acidic bogs demonstrates its remarkable edaphic plasticity. *R. tomentosa* likely relies on efficient nutrient resorption or specialized root-microbe associations to scavenge nutrients from these infertile substrates.

Rhodomyrtone is an acylphloroglucinol compound (Limsuwan et al. 2009) which is classified as phenolic. Phloroglucinols are secondary metabolites that occur naturally in certain plant species. The higher rhodomyrtone concentration found in plants growing in more shady conditions reflects a response to shade or shade-related factors since phenolics are pivotal compounds in the environmental stress response of plants. Examples of environmental stress for plants include UV radiation, drought, salt, heavy metal ions, and low temperature. Arena et al. (2017) reported high phenolic concentrations in plants exposed to high light levels. Exposed to solar UV-B radiation in open areas, plants produce flavonoids and other phenolic compounds to absorb the radiation. However, in shaded areas solar, UV-B levels are lower. Surprisingly, although phenolic acid contents are lower in coffee plants grown in 50-70% shade than in full sun, coffee plants grown in the shade of lychee trees (ca. 60% shade) had the highest phenolic acid level (Somporn et al. 2012). Thus, other factors than light levels could play roles in phenolic production. These factors could include plant-plant interactions, and microbial communities should also be investigated. It has been reported that phenolic production increases when plants have to cope with drought, and higher rhodomyrtone contents may be a response to water scarcity. However, since this plant is often found in sandy soil, which is normally water-deficient, it is not clear if water was scarcer in shaded or open areas in the present study. N, P, and K were non-significantly negatively correlated with rhodomyrtone.

According to Heimler et al. (2017), N, P, and K availability were inversely correlated with polyphenol production. The lack of significant correlation could be caused by the narrow and mostly very low range of N, P, and K at the study sites, which compiclates the detection of relationships. In other medicinal herbs like *Ocimum* L., soil organic carbon and microbial density were prime to the biosynthesis of secondary metabolites (Das et al. 2020). In

addition to abiotic stressors, plants produce phenolic compounds when coping with biotic stressors such as herbivores, nematodes, insects, viral, fungal, and bacterial pathogens, as well as competition from other plants (Tak and Kumar 2020). In this case, pathogen infection is one of the most possible reasons for the higher rhodomyrtone contents found in shaded areas, especially during heavy rains. Shade prolongs wetness, which is conducive to fungal growth (López-Bravo et al. 2012). At our study sites, heavy rain (up to 400 mm/month) was concentrated in a period of 3-4 months, while the rest of the year had light/no rain. Note that the correlation between percent cover and rhodomyrtone content was assessed pairwise.

Since natural populations of *R. tomentosa* have been reduced largely by land-use change (Xie et al. 2021), the cultivation of this shrub is necessary. Based on this study, the shrub ecologically thrives in open nutrient-poor sites. Chemically, secondary metabolite concentrations may increase under partial shade or in shaded microhabitats within those landscapes. *R. tomentosa* can be successfully cultivated in flat lowlands with sandy, nutrient-deficient soil of low pH. According to our dataset, plants should be grown under light shade to produce more rhodomyrtone. Liu et al. (2019) reported that moderate shading can enhance photosynthetic efficiency and reduce oxidative stress, which may increase rhodomyrtone accumulation in *R. tomentosa*. The area along the coast of Peninsular Thailand and other tropical coasts is the most suitable habitat for this medicinal plant. Additionally, its adaptability to acidic bogs and former sandbars suggests these habitats are highly suitable for cultivation, particularly where conventional crops struggle. Overall, the persistence of *R. tomentosa* along the shores of peninsular Thailand underscores its adaptability, but also highlights the threats posed by land-use changes. Conservation strategies should focus on maintaining existing groves, promoting habitat connectivity, and exploring its potential for sustainable cultivation in degraded lands. In addition, this shrub can potentially be intercropped within rubber or oil palm plantations. Future research should investigate the reproductive ecology, natural regeneration and population dynamics of *R. tomentosa* to inform effective conservation and restoration efforts.

The limitations of this study include its observational design, brief period of data collection, and absence of data on plant growth or yield under different light conditions. Further study should quantify the degree of fungal infection in natural populations in relation to light conditions and seasonal variations. In addition, an experimental study should be conducted on the association between the level of shade, degree of fungal infection and rhodomyrtone content.

In conclusion, *R. tomentosa* was found at 54 sites in Peninsular Thailand. The plant was present in flat and relatively open lowland areas, mostly below 100 m asl. The habitats could be classified as sandy areas close to the coast, degraded forest strips near riverbanks, and private land used for intensive agriculture. Soils were acidic and nutrient deficient. Soil texture was predominantly fine, medium and coarse sand. Leaf rhodomyrtone content was significantly positively correlated with percent canopy cover, but the correlation with soil physicochemical variables was non-significant. These findings highlight the ecological adaptability of *R. tomentosa* to low-nutrient, acidic sandy soils, particularly in coastal and riparian landscapes. The findings of this study indicate that this shrub should be grown in lowland, sandy, nutrient-poor soil of low pH for cultivation and it should also be grown under light shade to promote rhodomyrtone production. Protection of natural groves is also required to maintain genetic diversity.

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