ECOLOGICAL-EVOLUTIONARY RELATIONSHIPS IN *Passiflora alata* FROM RIO GRANDE DO SUL, BRAZIL

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ABSTRACT

The geographical distribution, ecological characteristics, flowering and fruiting times, and pollinating agents of *Passiflora alata* are considered and related to molecular genetic data gathered simultaneously. The first report on this species in Rio Grande do Sul was made in 1934, only in cultivated gardens. Approximately 20 years later, however, the species was already classified as *efferata* (wild) in Porto Alegre's suburbs. The data presented here, together with the DNA investigations, indicate that *P. alata* is actively colonizing previously unoccupied areas of this region.

Keywords: *Passiflora alata*, geographical distribution, phenology, colonization process, plant evolution.

RESUMO

Relações ecológico-evolutivas em *Passiflora alata* do Rio Grande do Sul, Brasil

A distribuição geográfica, as características ecológicas, as épocas de florescimento e frutificação, e os agentes polinizadores de *Passiflora alata* são considerados e relacionados a estudos genético-moleculares desenvolvidos simultaneamente. O primeiro registro da espécie no Rio Grande do Sul foi feito em 1934, apenas em área cultivada. Cerca de 20 anos depois, no entanto, a espécie já era classificada como *efferata* (selvagem) nos subúrbios de Porto Alegre. Os dados aqui apresentados, junto com as investigações de DNA, indicam que *P. alata* está colonizando ativamente áreas previamente não ocupadas desta região.

Palavras-chave: *Passiflora alata*, distribuição geográfica, fenologia, processo colonizador, evolução vegetal.

INTRODUCTION

As part of a long-term project of investigation of the genus *Passiflora* by our group (Muschner *et al*., 2003; Lorenz-Lemke *et al*., 2005) we studied *Passiflora alata* Curtis in detail in the Brazilian state of Rio Grande do Sul. The geographical proximity to the place where we work provided an opportunity to make detailed field and ecological observations, that can be related to the genetic-molecular studies that we were already making on this and related species.

P. alata is classified in the family Passifloraceae, occurring in the Atlantic Rain Forest, especially on the periphery of humid woods at low altitude, as well as in forest patches of varying size, near the coast. The species has a wide distribution in Brazil, being reported from the states of Bahia, Espírito Santo, Federal District, Mato Grosso do Sul, Minas Gerais, Paraná, Pará, Rio de Janeiro, Rio Grande do Sul, São Paulo and Santa Catarina. Moreover, it has been found in Argentina, Paraguay, and Peru (Killip, 1938; Feller, 1967; Sacco, 1980; Pessoa, 1994, 1997; Cervi, 1996, 1997; Cervi & Santos, 2000; Deginani, 2001; Bernacci, 2003).

The first published report of *P. alata* in Brazil dates from 1938, when Killip (1938) reported it as an

apparently native species in the majority of Brazilian states. Rambo (1951), Sacco (1962, 1980) and Feller (1967), however, referred to it as a cultivated species in Rio Grande do Sul, with the possibility of becoming wild; some years later Mondin (2001) classified it as subspontaneous. The factor that determined the present study was our observation that the species was abundant in the wild condition in many parts of the state, characterizing a possible case of a taxon in an active process of colonizing open spaces. Additionally, since the species is concentrated mainly in the central-eastern part of the Brazilian territory, the populations studied could represent a good model of species living at the borderline of their geographical range.

MATERIAL AND METHODS

The territory of Rio Grande do Sul is situated between 49° 43' and 57° 41' W. longitude and 27° 04' and 33° 45' of S. latitude, and represents the southern limit of the distribution of many tropical species, being described as a transition area between biogeographical provinces (Mondin & Baptista, 1996; Jarenkow & Sobral, 2000). According to Teixeira *et al.* (1986) Rio Grande do Sul is divided into six geomorphologic provinces (Araucaria Plateau, Campanha Plateau, Central Depression, Coastal Plain, Missions Plateau, and South Rio Grande Plateau) (Fig. 1) and seven phytoecologic facies (Deciduous Seasonal Forest, Dense Rain Forest, Mixed Rain Forest, Savannah, Semideciduous Seasonal Forest, Steppe, and Steppic Savannah), as well as two areas with special ecological conditions (Ecological Tension and Pioneer Formations). The latter roughly coincide with the geomorphologic boundaries.

The six geomorphologic and the nine phytoecologic regions of the state were searched, and *P. alata* material collected. For each specimen a sample was pressed and dried, and subsequently deposited at the ICN Herbarium, Botany Department, Biosciences Institute, Federal Uni-

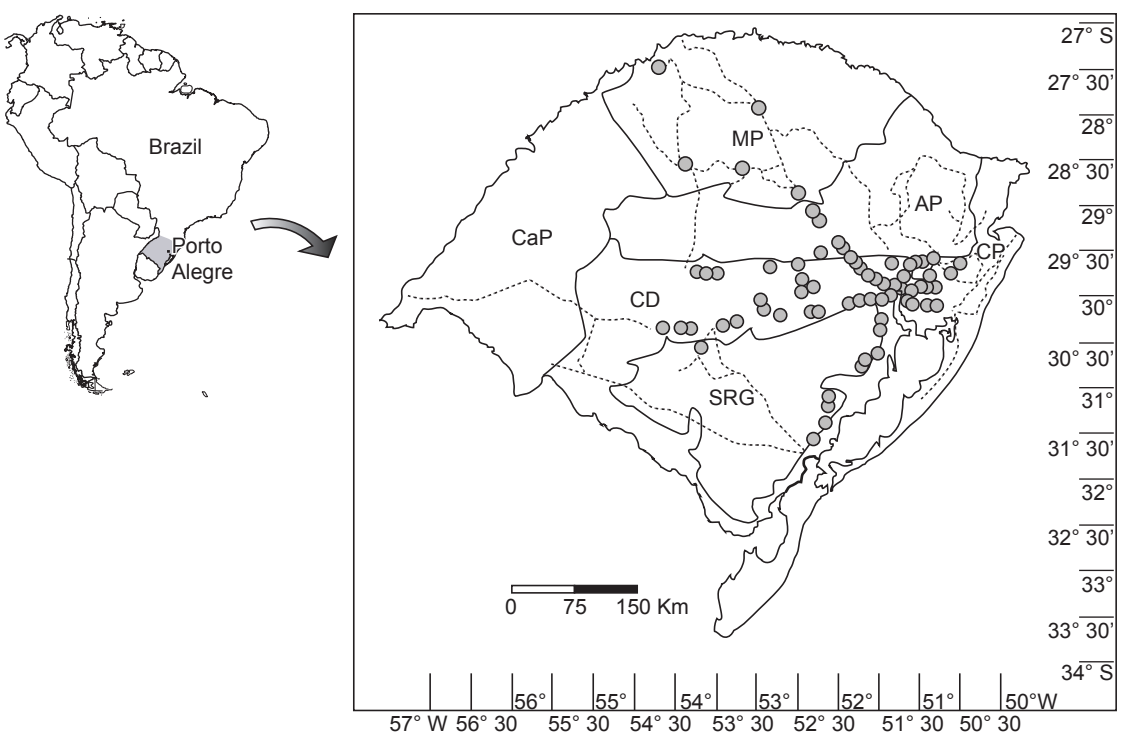

Fig. 1 — Map of South America (upper left) and enlarged map of Rio Grande do Sul, showing the places of collection (circles), the state's geomorphologic regions (AP: Araucaria Plateau; CaP: Campanha Plateau; CD: Central Depression; CP: Coastal Plain; MP: Missions Plateau; and SRG: South of Rio Grande Plateau) separated by full lines, and the routes followed in our field trips (dotted lines).

versity of Rio Grande do Sul. Subsamples were used for DNA studies, reported elsewhere (Koehler-Santos *et al*., 2005). Each collection point was georeferenced in accordance with standard procedures, using a Garmin GPS apparatus.

To access previous records of *P. alata* occurrence in Rio Grande do Sul, a survey was made (by electronic mail or personal visit) of the following herbaria: 1. HAS (Rio Grande do Sul Zoobotanical Foundation); 2. HUCS (Caxias do Sul University); 3. HURG (Federal University of Rio Grande Foundation); 4. ICN (Federal University of Rio Grande do Sul); 5. MPUC (Pontifical Catholic University of Rio Grande do Sul); 6. PACA (Anchieta Research Institute); 7. PEL (Federal University of Pelotas); 8. RSPF (Passo Fundo University); and 9. SMDB (Federal University of Santa Maria).

For each plant observed, besides the geographical coordinates, the following observations were registered: (a) presence/absence of floral buds or open flowers; (b) presence/absence of fruits; (c) when fruits were present, indications of predation; (d) presence/absence of pollinators and/or flower visitors; (e) environmental characterization (type of associated vegetation, evidence of human interference); and (f) presence/absence of associated *Passiflora* species.

RESULTS AND DISCUSSION

No records of *P. alata* were found in the HAS and MPUC herbaria, but a total of 37 occurrences were registered in the seven institutions listed in Table 1. The earliest dates from March 15, 1934, a record made by Rambo (1951), who found it in cultivated form in São Leopoldo, about 34 km north of Porto Alegre (PACA registration number 1275); the same researcher found wild *P. alata* in the suburbs of Porto Alegre on November 22, 1956 (PACA nº. 59215). After 1956, a series of occurrences have been documented of the species both in cultivated and wild plots.

Table 2 shows the places where we have collected *P. alata*, and Table 3 the routes we followed without finding it (see also Fig. 1). Listed in Table 2 are the 50 places of collection, with their geographical coordinates, that are shown graphically in Fig. 1. In all 192, specimens were collected and many more were observed. In many instances only one individual was sampled in a collecting site. *P. alata* was found in five of the six geomorphologic regions (exception: Campanha Plateau), and in eight of the nine phytoecologic regions (exception: Steppic Savannah). No morphologic variant was found in the state, confirming observations reported for other places in Brazil. Practically all plants were observed or collected in well-illuminated places disturbed by humans, like small woods near roads. No association with a specific type of vegetation was recorded.

Most plants were seen or collected in the Coastal Plain and Central Depression geomorphologic regions. In the Coastal Plain the main vegetation is of the Pioneer Formation type, and *P. alata* occurs in the more inland subtype, of riverine influence. In the Central Depression, plants of this species occur mainly in areas of Deciduous Seasonal Forests and Ecological Tension zones (with interpenetrating floras of two or more plant formations). Individuals were also collected in the Southern Rio Grande Plateau, a region characterized by a savannah-type vegetation, and eastern areas of the Semideciduous Seasonal Forest. On the Araucaria Plateau *P. alata* was seen or collected only in low altitude places. The lower number observed in the Mission Plateau region may be related to the type of economic activity prevalent there (grain cultivation) that extends the fields to quite near the roads. Both human presence (in the north grain production, in the south cattle rearing) and the type of dry climate prevalent in the Campanha Plateau may explain the absence of *P. alata* records there. This species occurs mainly on soils of the textural horizon type B, and to a lesser degree on litholic neosoils. The first are characterized by higher concentrations of clay than those found in under or upper strata, while the latter are very recent deep or plain formations which occur in several conditions of altitude and drainage (Streck *et al.*, 2002).

The plants were collected mainly along paved roads, and were seldom seen near unpaved ones, even when they occurred in nearby orchards. For example, our first trip along the RS 474 highway, which connects Santo Antônio da Patrulha to RS 239, occurred just after it was paved in November, 2001, and no *P. alata* specimens were found, even some distance from it. Two years later in October, 2003 several young plants, without flowers, were seen and collected. The difference may be due to the fact that along the paved roads

TABLE 1
Herbarium information for *P. alata* in Rio Grande do Sul.

Herbarium identification	Registration number	Locality	Date of collection	Status
HUCS	1771	Caxias do Sul	22/07/1986	cultivated
HURG	000723	Arroio Bolacha, Rio Grande	26/10/1983	wild
	000990	Vila da Quinta, Rio Grande	02/11/1982	wild
	001034	St. Hillaire, Viamão	17/03/1982	wild
	001998	Reserva Ecológica do Taim, Rio Grande	12/09/2000	wild
ICN	67234	Belém Velho, Porto Alegre	04/1987	no data
	94457	Estação Experimental, Viamão	09/01/1990	no data
	94773	Agronomia, Porto Alegre	06/1987	no data
	117541	Dom Pedro de Alcântara	24/05/1997	cultivated
	115084	Morro Grande, Viamão	21/10/1998	wild
	117715	Morro do Côco, Dom Pedro de Alcântara	05/12/1997	cultivated
	94775	Lomba do Pinheiro, Porto Alegre	07/1987	cultivated
	Nº II 27/26/1/3 Schultz 374	Porto Alegre	19/04/1938	cultivated
	4827	Viamão	06/1967	cultivated
	62573	Porto Alegre	20/03/1985	no data
	132158	Ponta Grossa, Porto Alegre	17/04/2003	wild
PACA	1275	São Leopoldo	15/03/1934	cultivated
	7183	São Leopoldo	06/09/1954	cultivated
	59215	Vila Manresa (Morro da Glória), Porto Alegre	22/11/1956	wild
	69744	I.A.S. (Instituto Agronômico do Sul), Pelotas	14/02/1962	cultivated
PEL	4548	São Lourenço do Sul	29/05/1963	cultivated
	10018	Between Km 321 and BR 116, Tapes	20/06/1988	wild
RSPF	6362	Espumoso	20/10/1998	wild
	7232	Montenegro	16/03/2003	wild
SMDB	4775	Boca do Monte, Santa Maria	31/10/1993	wild
	6510	Santa Maria	01/1996	wild
	3201	Jardim Botânico, UFSM	09/06/1987	no data
	8388	São João do Polêsine	27/01/2000	wild
	8384	São João do Polêsine	15/04/2000	wild
	8390	São João do Polêsine	no data	wild
	8391	São João do Polêsine	11/06/2000	wild
	8392	São João do Polêsine	01/11/1999	wild
	8394	São João do Polêsine	22/10/1999	wild
	8395	São João do Polêsine	27/11/1999	wild
	8397	São João do Polêsine	14/01/2000	wild
	8386	São João do Polêsine	29/02/2000	wild
	8400	São João do Polêsine	30/05/2000	wild

the cleaning of the adjacent terrain is more drastic, leading to the extinction of competitor species and the opening of space for *P. alata*.

Fig. 2 shows information concerning the phenology of *P. alata*, as observed in Rio Grande do Sul. The presence of only the vegetative state was observed in four months, two in winter (July, August) and two in summer (December, January). Floral buds and flowers were consistently seen in all other months, while fruits occurred in March, May, September, October, and November. Previous records by other authors indicate some variation among Brazilian regions both in flowering or fruiting times, with flowers present almost all year round, and fruit during five months (Sacco, 1962, 1980; Koschnitzke, 1993; Cervi, 1996, 1997; Varassin & Silva, 1999; Cervi & Santos, 2000; Bernacci, 2003).

The large flowers and odoriferous filaments of *P. alata* favor pollination by bees, and among its main pollinating agents are bees of the genus *Xylocopa* (Hymenoptera, Anthophoridae) (Sazima

TABLE 2
Collection sites for *P. alata* in Rio Grande do Sul.

Locality	Geographical coordinates[1]	Geomorphologic region
Esquina Gaúcha	27° 27'-54° 12'	Missions Plateau
Navegantes, Crissiumal	27° 30'-54° 07'	Missions Plateau
Sarandi	27° 58'-52° 55'	Missions Plateau
Ibirubá	28° 39'-53° 06'	Missions Plateau
Cruz Alta	28° 39'-53° 38'	Missions Plateau
Marques de Souza	29° 17'-52° 09'	Araucaria Plateau
São Vendelino	29° 22'-51° 23'	Araucaria Plateau
Bom Princípio	29° 26'-51° 21'	Araucaria Plateau
Três Coroas	29° 32'-50° 47'	Transition zone (CD-AP)
Estrela	29° 34'-51° 54'	Araucaria Plateau
Fazenda Vilanova	29° 35'-51° 50'	Araucaria Plateau
Igrejinha	29° 36'-50° 48'	Transition zone (CD-AP)
São Sebastião do Caí	29° 38'-51° 19'	Transition zone (CD-AP)
Venâncio Aires	29° 39'-52° 11'	Central Depression
Rolante	29° 40'-50° 40'	Coastal Plain
Portão	29° 40'-51° 16'	Transition zone (CD-AP)
Tabaí	29° 40'-51° 45'	Araucaria Plateau
Taquara	29° 42'-50° 49'	Coastal Plain
Taquari	29° 42'-51° 51'	Central Depression
Santa Maria	29° 43'-53° 40'	Central Depression
Pinheirinhos, Santo Antônio da Patrulha	29° 44'-50° 37'	Coastal Plain
Restinga Seca	29° 44'-53° 27'	Central Depression
Novo Cabrais	29° 45'-53° 03'	Central Depression
Montenegro	29° 49'-51° 24'	Central Depression
Morungava, Gravataí	29° 52'-50° 54'	Coastal Plain
Itacolomi, Gravataí	29° 52'-50° 59'	Coastal Plain
Santo Antônio da Patrulha	29° 53'-50° 32'	Coastal Plain
Nova Santa Rita	29° 53'-51° 15'	Central Depression
Glorinha	29° 54'-50° 43'	Coastal Plain
Canoas	29° 54'-51° 14'	Central Depression
Gravataí	29° 57'-50° 57'	Coastal Plain
Porto Alegre	30° 02'-51° 12'	Coastal Plain
Eldorado do Sul	30° 05'-51° 37	Central Depression
Viamão	30° 06'-50° 59'	Coastal Plain
Capão da Porteira, Viamão	30° 07'-50° 41'	Coastal Plain
Águas Claras, Viamão	30° 09'-50° 55'	Coastal Plain
Butiá	30° 09'-52° 01'	Central Depression
Minas do Leão	30° 09'-52° 04'	Central Depression
Guaíba	30° 12'-51° 24'	South Rio Grande Plateau
Cachoeira do Sul	30° 14'-52° 42'	Central Depression
Capané, Cachoeira do Sul	30° 17'-53° 06'	Central Depression
Barra do Ribeiro	30° 18'-51° 25'	South Rio Grande Plateau
Caçapava do Sul	30° 37'-53° 32'	South Rio Grande Plateau
Sentinela do Sul	30° 39'-51° 34'	South Rio Grande Plateau
Balneário Pinvest, Tapes	30° 40'-51° 23'	Coastal Plain
Vila Arroio Teixeira, Tapes	30° 40'-51° 23'	Coastal Plain
Eldorado do Sul	31° 03'-51° 20'	South Rio Grande Plateau
São Lourenço do Sul	31° 14'-52° 01'	South Rio Grande Plateau
Cerrito Alegre, Pelotas	31° 33'-52° 14'	South Rio Grande Plateau
Vila Assumpção, Pelotas	31° 46'-52° 20'	South Rio Grande Plateau

[1]Geographical coordinates: south (S); and west (W).

& Sazima, 1989; Koschnitzke, 1993, Koschnitzke & Sazima, 1997; Varassin & Silva, 1999; Varassin *et al.*, 2001). On the other hand, Varassin & Silva (1999) and Varassin *et al.* (2001) observed that bees of the genus *Apis* (Hymenoptera, Apidae) are predators of *P. alata* plants, since they take pollen from it, but do not perform the pollinization process. Our observations partially agree with this information. We continuously followed one *P. alata* plant cultivated on the campus of our university where our Department is located, commonly visited by *Apis* bees, and observed that although the fruit is formed it never matured over the four years (2000-2004) of our observation. However, in wild specimens distributed in woods at the periphery of the campus, fertile plants occur which are visited by both *Apis* and *Xylocopa* bees.

Seed dispersion in the Passifloraceae is generally made by birds and bats, attracted by the color and smell of the mature fruit (Semir & Brown, 1975); however, small terrestrial mammals were also observed eating *Passiflora* fruit (Williams *et al.*, 2000). Fruit collected by us during the trips showed tooth marks that were identified by our colleagues, A. Kindel and T. R. O. Freitas, as being made by the opossum *Didelphis albiventris* and the arboreal rodent *Oryzomys subflavus*. Therefore, these animals, in addition to other still unidentified agents, should be considered as seed disseminators and predators in our region.

The molecular-genetic studies we performed on *P. alata* are being reported in full elsewhere (Koehler-Santos *et al.*, 2005). However, a description of the main findings related to the present observations is in order. Briefly, we studied representatives of all populations found in Rio Grande do Sul, in relation to three nuclear DNA systems [ribosomal Internal Transcribed Spacers or ITS; a partial segment of the glyceraldehyde 3-phosphate dehydrogenase (*G3pdh* or *gpd*), and the second intron of the LEAFY genes], as well as eight plastid regions. While the latter did not show variability, the three nuclear genes provided important information. Characteristics of variability from all three clearly indicated that *P. alata* is experiencing a population expansion. In addition, their high intrapopulation variance and the absence of a clear geographical structure, also suggest that the *P. alata* populations sampled have arrived recently in their present areas of distribution.

The effective invasion of an environment by new species is influenced by three factors: the number of individuals (or their gametes) which are introduced; the internal characteristics of the invading species; and the environmental susceptibility to the invasion of new species. The latter involves many factors, such as climate, the amount of environmental disturbance due to human presence or its products, and the competitive ability of the resident species. Other factors are soil type, presence or absence of herbivores, pathogenic agents, and facilitating effects of the resident vegetation (Decker, 1936; Lonsdale, 1999; Davis *et al.*, 2000). In the specific case under discussion, it is possible that the presence of dispersion and pollinization agents that are already acting on other native species of *Passiflora* present in Rio Grande do Sul may have facilitated the colonization process of *P. alata*. It is important to mention that although these other species of *Passiflora* occur in the state, they are never found in association with *P. alata*. Therefore, the latter might be competing with other taxa. Historical, genetic, morphological, and the ecological characteristics presented in this paper, together with the easy adaptation of *P. alata* to cultivation, all indicate its plastic nature and suggest that the taxon is undertaking an active process of colonization of new territories.

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TABLE 3
Places where *P. alata* was not found in Rio Grande do Sul[1].

Road	Detail	Date
RS 344	Between Santa Rosa and Entre-Ijuis	apr/2002
RS 155	Between BR 468 and Ijuí	apr/2002
BR 468	Between Palmeira das Missões and RS 155	apr/2002
RS 569	Between Palmeira das Missões and Sarandi	apr/2002
BR 285	Between Lagoa Vermelha and Vacaria	mar/2004
RS 324	Between Passo Fundo and Veranópolis	mar/2004
BR 386	Between Carazinho and Pouso Novo	apr/2002
BR 285	Between Entre-Ijuis and Ijuí	apr/2002
BR 158	Between RS 155 and Cruz Alta	apr/2002
BR 116	Between Vacaria and Caxias do Sul	mar/2004
RS 223/BR 377	Between Cruz Alta and Tio Hugo	apr/2002
BR 158	Between Cruz Alta and Santa Maria	nov/2003
VRS 24	Between Ibirubá and Fortaleza dos Valos	oct/2003
RS 110	Between Bom Jesus and São Francisco de Paula	jul/2003
RS 122	Between Ipê and Caxias do Sul	mar/2004
RS 020	Between Cambará do Sul and São Francisco de Paula	jun/2003
RS 334	Between BR 386 and RS 223	oct/2003
RST 453	Caxias do Sul	mar/2004
RS 122	Between Caxias do Sul and Farroupilha	mar/2004
BR 116	Between Caxias do Sul and Nova Petrópolis	mar/2004
RST 453	Between Bento Gonçalves and Farroupilha	mar/2004
RST 470	Between Bento Gonçalves and São Vendelino	mar/2004
RS 235	Between Nova Petrópolis and Gramado	mar/2004
RS 389	Between Torres and Imbé	feb/2004
RS 474	Between Santo Antônio da Patrulha and RS 239	nov/2001
RS 484	Between Maquiné and Barra do Ouro	mar/2002
BR 101	Between Maquiné and Capivari do Sul	mar/2002
RS 030	Between Santo Antônio da Patrulha and BR 290	nov/2001
BR 290	Between Porto Alegre and Uruguaiana	jul/2002
BR 158	Between BR 293 and BR 290	aug/2002
BR 153	Between BR 290 and BR 392	oct/2002
BR 392	Between BR 153 and Caçapava do Sul	oct/2002
RS 625	Between RS 353 and BR 392	oct/2002
BR 392	Between BR 290 and Pelotas	sep/2002
BR 293	Between Santana do Livramento and Pelotas	aug/2002

[1]The information given refers to field notes registered during the trips; some local roads without identification could not be included in this list. The road codes could have changed in the intervening years.

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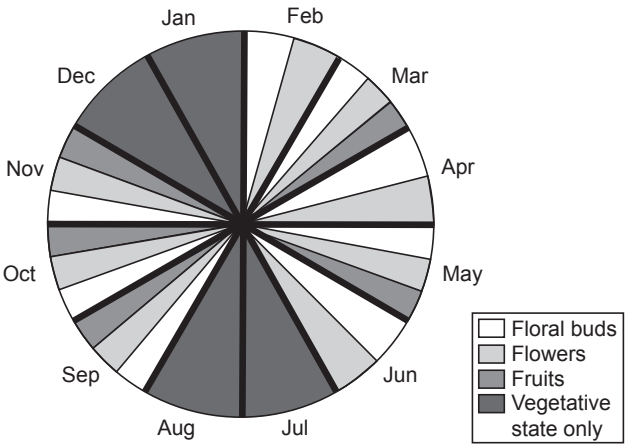

Fig. 2 — Phenology of *P. alata* observed in the state of Rio Grande do Sul.

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