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# Does the Growth Rate of Different Reproductive Modes of an Introduced Plant Cause Invasiveness?

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**Abstract:** Invasive species are often associated to specific life historical traits. However, no studies have quantitatively compared different propagation capacities within the same species. According to its various reproductive modes (seedling, sprout, terrestrial layering, cutting) and its wide colonization (from 0 to 1700 m a.s.l.), the Asian bramble *Rubus alceifolius* is an ideal model to study growth rate and thus better understand plant invasiveness. Growth of different reproductive modes in contrasting environmental sites during time was measured. Results showed that, whatever the study site, sexual maturity of seedling appeared longer (>2 years) than sexual maturity of new vegetative stems formed by sprouts and terrestrial layering (<1 year). A significant difference of growth rate was observed on dry coast at low elevation where *R. alceifolius* grows slowly and can't be considered as invasive in this region. In all studied sites, cuttings didn't grow. The process of the plant colonisation can be recount. After initial colonization by seedlings, vegetative growth favour monospecific stands formation and *R. alceifolius* maintenance during time. Growth comparisons were argued between native and introduced areas.

**Key words:** Alien plants, biological invasion, life historical traits, juvenile period, *Mascarene archipelago*, Réunion island, *Rubus alceifolius* Poiret

# INTRODUCTION

Fast growth from seedling to sexual stages (i.e., short juvenile period), capacity for both sexual and asexual reproduction, pronounced phenotypical plasticity and high tolerance for environmental heterogeneity are among factors seen as leading to invasion success<sup>[1,2]</sup>. Several researchers have analyzed life historical traits of particular invasive species[3-6]. However, many of these ideas have not been tested quantitatively<sup>[5]</sup>. Careful review of aliens worldwide demonstrates that no single life history trait predominates in aggressive invaders [7]. Some species that combine both long-distance and effective short-distance ability are among the most successful invaders<sup>[8,9]</sup>. These species can use different strategies in contrasting habitats. For example, the invasion of coastal plant communities in California by Carpobrotus edulis is a habitat-specific process depending on soil disturbance, herbivory and identity of competitors[7]. Alternative reproductive strategies (i.e. allocation of resources to sexual reproduction or vegetative propagation) are known to affect the outcome of invasion[7]. Pyšek[10] also

suggested analysing the success of different clonal forms. Therefore, it is decided in this study to better understand colonization capacities of invasive non-indigenous plants through growth measures of their different reproductive modes. For that, growth vigour of Rubus alceifolius according to its various reproductive mode was measured and areas where it is able to colonize was measured. Indeed, this species seems to be an ideal model in the study of these processes thanks to its numerous reproductive modes and its wide colonisation[11,12], but also because of the study area, which is an oceanic island: Réunion Island (Mascarene archipelago, Indian Ocean). Island ecosystem has been recognized as highly vulnerable to invasions<sup>[13,14]</sup>. Since human settlement on Réunion, during the 17th century, more than 2000 plants species have been introduced[15], 432 were naturalized and 62 were considered as very invasive[16]. Among these, Rubus alceifolius is native of Southeast Asia and was introduced in Réunion in the 1840s<sup>[17]</sup>. This species currently grows in a broad range of habitats[16]. Baret et al.[12] confirmed that Rubus alceifolius can invade Réunion Island from sea level to 1700 m a.s.l. probably

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due to its phenotypic plasticity and various reproductive modes: seedlings, sprouts, terrestrial layering<sup>[11]</sup> and cuttings<sup>[18]</sup>. Certainly, several studies showed that the number of invasive species is often associated to an important sexual reproduction, an effective vegetative reproduction and a short juvenile period<sup>[5]</sup>. But no studies have quantitatively compared the different capacities of propagation within the same species. The growth study of R. alceifolius, was conducted (1) to compare the different growth capacities of this species according to the reproductive modes and to the sites, (2) to know the juvenile period length of this plant and to know if the various modes of asexual reproduction can or not shorten this duration (3) to clarify the theories of prediction of invasive species.

# MATERIALS AND METHODS

**Study site:** The study was carried out in Réunion Island (21°06' S, 55°32' E) in contrasted sites. On the windward coast (eastern), 3 sites were chosen: St-Philippe (20E), Grand-Etang (550E) and Petite Plaine (1200E). On the leeward coast (western), 2 sites were selected: Etang-Salé (20W) and Makes (950W). Characteristics of studied sites are specified in Table 1.

Rubus alceifolius Poiret is a giant bramble which prefers wet areas. It proliferates on the east and south-east coasts, which record the strongest precipitation (annual average between 3 and 18 m)[19], while it appears only from 500 m a.s.l. in the west coast ravines which is more dry (below 500 m elevation, annual average precipitation < to 500 mm). This species is a shrub with arched branches, which can reach 10 m length and root on its apex. An individual of R. alceifolius grown from seed can be regarded as rootstock that bears shoots of various sizes, which are emitted successively during development<sup>[11]</sup>. This study, compared the seedlings (individuals coming from seed), sprouts (stems coming from root-stock), cuttings (stems portion) and terrestrial layering (also called tip-rooting axe which form a new self supporting stem having a development similar to a sprout)[11].

The monitoring growth of the different reproductive modes of *Rubus alceifolius* was measured in open areas, which are preferentially colonized by this invasive plant species<sup>[20]</sup>.

# Monitoring growth of seedlings, cuttings and sprouts:

Twenty individuals for each reproductive modes were set up in December 1999 in the sites of St-Philippe (20E), Etang-Salé (20W) and Makes (950W). The different individuals installed (all <5 cm high at the beginning of

Table 1: Studied sites characteristics: altitude (Alt), coast © -W for the western coast and E for the eastern coast-, mean annual temperature (T) and total annual precipitation (P) are mentioned for each study sites. (A code for each site is given and will be used in the other tables and in the text)

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Code	Sites	Alt (m)	С	T (°C)	P (mm)		
20W	Etang-Salé	20	W	25.0	500		
500E	Grand-Etang	500	E	20.4	5600		
950W	Makes	950	W	16.5			
1200E	Petite Plaine	1200	E				
20E	St-Philippe	20	E	24.5	3850		

the experiment) come all from Mare Longue (Near St-Philippe on southeastern of the island at 220 m a.s.l.). They were collected on young regeneration forestry plots. For the sprouts, the stems already in growth before the experiment were all cut to 20 cm. Buds only located on the stock of each plant are preserved. Plants were all put out into pots (40 L) beforehand filled by a mixture of ground, compost and sable (3x1/3). Moreover, only 12 seedlings and 15 sprouts grew at Etang-Salé (20W), 18 sprouts grew at Makes (950W) and 7 at St-Philippe (20E). None cuttings grew in the different studied sites. Therefore, this reproductive mode could not be integrated in the results.

Monitoring growth of terrestrial layering: It's the new stem formed that it measured in this study. As we didn't want to disturb relationship between this new stem and it parent (nutritive exchange it's possible between both), we monitored it growth on the field. Moreover, as Rubus alceifolius was not present on the leeward lowland and as we would like to observe attitudinal variation, we measured terrestrial layering growth in 2 sites localised the windward coast (eastern). Unfortunately, only 9 terrestrial layering grew on the first site (Grand-Etang, 500E) and have been involuntary uprooted in June 2000. Only the other site, Petite Plaine (1200E) is considered in this study. Nevertheless, only 10 terrestrial layering grew on this last site.

**Parts of root system:** Forty were also cut and put into the ground. None of these parts did produce new plants. These data will not be mentioned in the results but inform about the incapacity of *R. alceifolius* to be propagated in that way.

Monitoring growth: For all plants, monitoring growth was measured monthly during 1.5 years (from December 1999 to July 2001, including two fruit seasons). The stock diameter and the stems length of each plant were measured. When many stems grown on the same stock, stems length include the length of all the stems. Moreover, as stocks were not always circular, their diameter was calculated according to the following formula:  $2*\pi*(length + width)/2$ .

Statistical methods: Statistical analysis has done on the similar sites where seedlings and sprouts were located (20E, 20W and 950W). The stem length has been statistically analysed, between the different reproductive modes (sprouts and seedlings) and sites, 3 months after the beginning of the experiment (March 2000), in the middle (December 2000) and at the end (July 2001). The stocks diameter were statistically analysed at the beginning of the experiment (December 1999), 1 year later (December 2000) and at the end of the experiment (July 2001).

Data were analysing using Statistix 7 software<sup>[21]</sup>. For each variable, normality was tested using the Shapiro-Wilk Normality test. Stocks diameter values were normally distributed. The data concerning the length of the stems were also normally distributed at the beginning of the experiment, but need to be transformed (logarithmic) to be normally distributed in December 2000 and July 2001. A Mann-Withney test enabled us to distinguish 2 to 2 the data between sites and reproductive modes. A 2 ways-ANOVA enabled us to compare the reproductive modes effect, sites and their interactions.

## RESULTS

Means of cumulated stems length and stocks diameter obtained show variations between sites and modes (Fig. 1 and 2).

**Reproductive modes effect:** For each census (from March-2000 to July-2001), a two-way ANOVA indicated that means of cumulated stems length and means stocks diameter are significantly different between both reproductive modes (Table 2 and 3). A Mann-Withney test indicated that these differences are significantly bigger for sprouts than for seedlings (Table 2 and 3).

**Site effect:** Concerning means of cumulated stems length, a two-way ANOVA shows significant differences between sites for each census (Table 2). Nevertheless, the Mann-Withney test indicated that differences are only significant 1 year and 1.5 years after the beginning of the experiment which start in December 1999- for sprouts (For example in July 2001: 1839.4 cm±1119.7 at St-Philippe (20E), 1215.8 cm±253.3 at Makes (950W) and 148.2±70.7 at Etang-Salé (20W) and 1.5 years for seedlings (104.5 cm±21.5 at St-Philippe (20E), 582.9 cm±277.9 at Makes (950W) and 9.5±2.3 at Etang-Salé (20W), in July 2001).

Concerning means of stocks diameter, a two-way ANOVA shows significant differences between sites after 1 year growth (since December 2000, Table 3). Moreover,

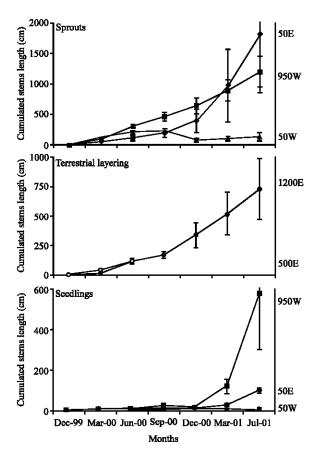


Fig. 1: Cumulated stem length (means±SE) of sprouts, seedlings and terrestrial layering located in different sites during 1.5 years monitoring. See Table 1 for code sites abbreviations

a Mann-Withney test shows significant differences 1.5 years after the beginning of the experiment for sprouts stocks (57.77 cm±3.36 at Makes (950W) against Etang-Salé (20W) 47.35 cm±3.49) and for seedlings stocks (21.99 cm±2.41 at Makes (950W), 9.25 cm±0.58 at Etang-Salé (20W) and 10.05 cm±0.21 at St-Philippe (20E)).

# Interactions between sites and reproductive mode:

For cumulated stems length data (Table 2), three months after the beginning of experiment (March 2000), a 2 ways-ANOVA shows a small interaction between sites and reproductive modes (F = 3.3). One year after (December 2000), this test indicates significant differences between these 2 factors (F = 25.3). One year and a half after (July 2001) plants installation, interaction between these 2 factors is not significant (F = 0.9).

For stocks diameter data (Table 3), interactions between these 2 factors are significant during study (respectively, F=4.0 at the beginning, F= 224.5-1 year later and F= 182.1-1.5 years after).

Table 2: Cumulated stems length (means in cm±SE) between reproductive modes (seedlings and sprouts) and sites (20W, 20E and 950W). A change in letter(s) means that values are significantly different at the 5% level according to a Mann-Withney test

					F-values	F-values		
		Sites			2 ways- ANO	2 ways- ANOVA		
Dates	Modes	20W	20E	950W	Modes	Sites	Modes* sites	
03/00	seedlings	8.9±0.4a	7.9±0.5a	10.6±1.0a	327.8***	3.6*	3.3*	
	sprouts	127.2±14.9b	75.2±21.9b	106.8±14.0b				
12/00	seedlings	24.5±9.5a	12.6±1.3a	19.5±2.3a	539.7***	29.9***	25.3***	
	sprouts	88.8±22.5b	334.3±230.0b	648.3±131.8c				
07/01	seedlings	9.5±2.3a	104.5±21.5b	582.9±277.9c	73.4***	70.8***	0.9 ns	
	sprouts	148.2±70.7b	1839.4±1119.7cd	1215.8±253.3d				

Table 3: Stock diameter (means in mm±SE) during time. A change in letter(s) means that values are significantly different at the 5% level according to a Mann-Withney test

Dates	Modes				F-values		
		Sites			2 ways- Anova		
		20W	20E	950W	Modes	Sites	Modes* sites
12/99	seedlings	2.27±0.08a	1.99±0.09b	2.17±0.11b	173.3***	1.0ns	4.0*
	sprouts	38.45±2.45f	36.43±2.39f	$37.28\pm2.74f$			
12/00	seedlings	6.40±0.39c	7.12±0.40c	8.50±0.57cd	668.4***	187.2***	224.5***
	sprouts	46.52±3.08g	41.86±2.83fg	46.34±4.43g			
07/01	seedlings	9.25±0.58d	10.05±0.21d	21.99±2.41e	224.0***	54.9***	182.1***
	sprouts	47.35±3.49g	48.74±3.79gh	57.77±3.36h			

F values from a two-ways Anova (sites and reproductive modes effects and their interactions): \*\*\*, p<0.001; \* p<0.05; ns, non-significant

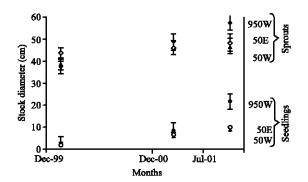


Fig. 2: Stock diameter (means±SE) of sprouts and seedlings located in different sites during 1.5 years monitoring. See Table 1 for code sites abbreviations

Flowering and terrestrial layering appearance: Among different reproductive modes, only sprouts produced floral buds and fruits. Only 2 sprouts (among 15) fruited at Etang-Salé (20W), 3 (among 7) at St-Philippe (20E) and 10 (among 18) at Makes (950W). The production of floral buds and fruit is observed 13-16 months after the beginning of experiment and doesn't start in the same moment in the different sites (in January 2001 at St-Philippe (20E), 1 month later at Etang-Salé (20W) and in April at Makes (950W)). In the 3 sites studied, flowering is still present until July-August 2001. Among flowering individuals, means number of floral buds during flowering period is more important at St-Philippe (20E) (302±230 buds, n = 3) than at Etang-Salé (20W) (94±19 buds, n = 2)

and Makes (950W) (39 $\pm$ 13 buds, n = 10). Among fruiting individuals, means number of fruits produced is, respectively 31 $\pm$ 24 (St-Philippe (20E), n = 3), 11.5 $\pm$ 4.5 (Etang-Salé (20W) n = 2) and 5.3 $\pm$ 1.4 (Makes (950W), n = 4).

Terrestrial layering are formed in April at St-Philippe (20E) and 1 month later at Makes (950W). None terrestrial layering was observed at Etang-Salé (20W).

#### DISCUSSION

# From seedlings to adult stage

Seedlings development: Whatever study sites are, juvenile period was longer than 2 years. Personal observations indicated that the first flowering period begin 2 years after seedlings (in January 2002 at St-Philippe (20E) and April 2002 at Makes (950W)). Duration of this period can be explained by the development of successive stages morphologically and architecturally distinct from sexual adult stage[11]. These results are in agreement with different theories emitted on invasive species, in which the relatively short juvenile period is one of major features of effective invasion[6,22]. Present observations confirm that juvenile period is closely correlated with life form. Rejmanek and Richardson<sup>[22]</sup> indicated 'r-strategists' as best invaders. Rubus alceifolius, can be included in 'r-strategists' group. Having a life form between a bush and a liana, this species can easily invade cultivated lands (opening areas) and indigenous forests<sup>[11]</sup> in less than three years (in this study, two years to reach mature stage and one new year to form mature stems coming from terrestrial layering or sprouts). Nevertheless, although speed, *R. alceifolius* establishment differed according to sites. Seedlings growth and stock development of *R. alceifolius* were slow when it develops in lowland dry site Etang-Salé (20W), faster in wet lowland St-Philippe (20E) and significantly more important in wet highland Makes (950W) (Table 2 and 3). Even if *R. alceifolius* seedlings growth is quicker in wetlands, it can also invade dry lands but mainly in gullies below 500 m (Personal observation).

Sprouts development: The development of a stem formed by a stock can be summarized as follows[11], Stem initially passes by a vertical development before curb gradually and root on it extremity. It is on the arched zone that the floriferous stems were formed (in October-November-December). The development of these stems is fast. They produce flowers and fruits firstly at low elevation (from February to July 2001, 20E and 20W) and later at more higher altitude (April to July-August 2001, at 950W site), respectively 12 and 14 months after sprouts establishment. Sprouts growth varied according to sites. At Etang-Salé (20W), majority of stems were vertical because sun burnt their extremity and sometimes all the stems. Only few floral buds and fruits have been developed on secondary stems. The number of buds and fruits was thus lower than this observed at Makes (950W) and St-Philippe (20E). The main stem usually rooting at its extremity[11] was not observed in the 20W site. Terrestrial layering were observed in the two other sites. Those began their formation in April at St-Philippe (20E) and in May at Makes (950W). This apical rooting could be correlated with luminosity reduction[23] and duration of day (shortening in winter)[24]. It could also include temperature as possible factor responsible of the flowering-fruiting formation shift between low and high lands[12,25], as it is the major parameter that varies with elevation. Present results show that cumulated stems of terrestrial layering are less long than those formed by sprouts (Fig. 1). This difference can be explain by the fact that a sprout form several stems at the same time while a terrestrial layering form only one stem during the first vear[11].

Why *R. alceifolius* was invasive?: possible process of its colonization: Seedlings located in open areas were able to fruit after 24 months. Having an important fructification period in lowland (below 1100 m a.s.l.), *R. alceifolius* fruits are disseminated by barochory<sup>[12]</sup> and ornithochory (probably until 1700 m a.s.l.)<sup>[26]</sup>. Because this species do

not fruit above 1100 m a.s.1.[12], vegetative reproductive modes have an important role in its invasiveness. Once installed in a new site after seed dissemination, R. alceifolius gradually develops according to the process described by Baret et al.[11,25] and quickly forms monospecifics stands (in 3 years) by tangle of many new vegetative stems formed by terrestrial layering and sprouts. Each of these new stems fruit actually after only one year in lowland and form new terrestrial layering and sprouts in low and high lands. The sexual maturity is thus shortened. In relation with our results, Pysek<sup>[10]</sup> thinks that once established, clonal plants seem to be more persistent and competitive which leads to an effective occupation of available space. Prach and Pysek[27] also evoked that the role of extensive clonal dispersal in succession is evident in both early stages (due to rapid capture of available area made by disturbance) and in late-successional stages (due to rapid filling of gaps in more or less closed vegetation cover).

Do growth variations exist between individuals located in introduced and native areas?: Strength and advantage of plants introduced into new habitats can be due to their establishment in a more favourable environment, where there is no pressure from phytophagous and pathogenics<sup>[28,29]</sup>. Thus, in absence of pathogenics and herbivores, it is often described that invasive plants are (i) higher<sup>[29]</sup>, although there is no general tendency<sup>[30]</sup>, (ii) live longer[31] and (iii) generally show considerable vigorous growth in their introduced area compared to their native area<sup>[32,33]</sup>. In Réunion Island, Attié et al.<sup>[34]</sup> surveyed phytophagous of most invasive plants. Even if quantitative measures will need to be Bourgeois<sup>[35]</sup> observing phytophagous pathogenics on R. alceifolius in Réunion, noted less damage than those observed in their native areas. Furthermore, stems growth comparisons of sprouts coming from Réunion and transplanted in Sumatra (native area) grow quicker than those coming from Sumatra or other native areas (Rock Desmier de Chenon, pers. com.). These data would confirm the results obtained by Amsellem et al.[36] who can genetically distinguish plants introduced on Réunion from those present in their native areas.

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