

***Actinidia* interspecific hybrids: Valuable resources for the selection and breeding of kiwifruit rootstocks**

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Abstract

Interspecific hybridization is an effective way to create desirable rootstocks for grafting fruit crops such as kiwifruit. Previous studies showed that interspecific hybrids in the genus *Actinidia* could be obtained through *in vitro* embryo culture. In attempts to develop vigor-controlling rootstocks, conventional intraploid crosses between two species that differ in the vigor of their root systems—*A. arguta* (Issai selection) and *A. chinensis* var *deliciosa* (four male genotypes)—were successfully performed without resorting to embryo rescue. A wide variation in root architecture characteristics was detected among the hybrid progenies. The identification of hybrids with less vigorous root systems than those of *A. chinensis* var *deliciosa* further highlights the potential of the intraploid hybridization between these species to develop rootstocks with size-controlling potential for kiwifruit. Statistically significant effects of male parent on seed set (xenia), and percentage of germination and normal hybrid seedlings were also detected in this investigation.

Key words: Rootstock breeding, conventional interspecific crosses, *Actinidia chinensis* var *deliciosa*, *Actinidia arguta*, male parent effects, root system analysis

Introduction

The kiwifruit is a novel fruit crop of temperate climate with remarkable nutraceutical properties such as high content of vitamin C, polyphenols and actinidine (Huang, 2016). It belongs to the genus *Actinidia*, which has a high basic chromosome number ($x=29$) and a wide variation in ploidy (Ferguson and Huang, 2007).

Actinidia species are perennial and functionally dioecious (Ferguson, 2007). For many years, the emphasis in kiwifruit breeding was significantly strong on the species complex *A. chinensis* Planch., which includes two main varieties: *A. chinensis* var. *chinensis* ($2n=2x=58$ and $2n=4x=116$, abbreviated as Ach) and *A. chinensis* var. *deliciosa* ($2n=6x=174$, abbreviated as Ad), which produce yellow and bright-green fleshed fruits, respectively (Liu *et al.*, 2015). Other *Actinidia* species are still not widely grown crops such as *A. arguta* (Siebold and Zucc.) Planch. ex Miq. ($2n=2x=58$, $2n=4x=116$ and $2n=6x=174$, abbreviated as Aa), which produces small smooth-skinned fruits (Baby kiwifruit) that can be eaten with the peel like a “snack” (Kataoka *et al.*, 2010).

The economic value of kiwifruit fruits could be affected by an excessive vegetative vigor (Broom *et al.*, 2000; Cooper *et al.*, 2007; Patterson and Currie, 2011). In attempts to control this vegetative growth, two approaches based on the pruning practices have been considered: (1) shoot pruning by extensive and frequent removal of both shoots and leaves which has generated a huge economic impact on kiwifruit growers (Miller *et al.*, 2001), and (2) root pruning by removal of a part of the root system (Black *et al.*, 2011; 2012). The latter approach is based on the reduction in root area which modifies carbohydrate partitioning, yields larger fruit with higher carbohydrate content (Patterson *et al.*, 2009) and reduce vegetative growth due to a hydraulic effect (Black *et al.*,

2012). An alternative to reduce root area besides root pruning would be to use rootstocks that provide smaller root systems than the own-root systems of the kiwifruit vines (potential vigor-controlling rootstocks).

Some *Actinidia* species have been tested as rootstocks (Wang *et al.*, 1994; Clearwater *et al.*, 2004, 2006; Thorp *et al.*, 2007; Mi *et al.*, 2013; Huang, 2016), but none has been available to control scion vigor in kiwifruit (Clearwater *et al.*, 2004, 2006). To be taken into account is that the healthy kiwifruit vines of both Ad and Ach have many more roots than necessary for water uptake under normal growing conditions (Reid and Petrie, 1991; Black *et al.*, 2011), whereas Aa has root systems less developed than those of Ad, as shown by Klages *et al.* (1999), highlighting a selection called Issai that is less vigorous than the rest of the cultivars of the same species (Strick, 2005). In this context, it should be expected that interspecific hybridization between Ad (or Ach) and Aa would generate useful root variability for the selection of potential size-controlling rootstocks.

Analysis of phylogenetic relationships between *Actinidia* species provides convincing evidence of frequent interspecific hybridization in the wild (Chat, 2004). However, reproductive isolation, especially postzygotic reproductive barriers, is thought to be largely responsible for the co-occurrence of cytotypes (Liu *et al.*, 2010). Ploidy variation can make the crossing in *Actinidia* difficult (Huang and Liu, 2014). Many interspecific crosses have been attempted (Harvey *et al.*, 1995; Monet *et al.*, 1997; Hirsch *et al.*, 2001; Cotrut *et al.*, 2013, among others), although successful fruit setting and seed formation depended on the particular genotype combination in each case. In interspecific crosses, that have failed, fruit set did not occur, or if it did, the seeds were empty of embryos and/or of endosperm (Hirsch *et al.*, 2001).

In *Actinidia*, as in many other genera, crosses between species at the same level of ploidy are more successful than crosses carried out using species with different ploidy level (Hirsch *et al.*, 2001). In the case of the intraploid hybridization between Aa and Ad, Issai selections of Aa are hexaploid like Ad (Kataoka *et al.*, 2010; Huang, 2016) and could be used as a female parent. These selections have been claimed to be hermaphrodite and self-setting by some researchers (Kempler and Kabaluk, 1995; Kabaluk *et al.*, 1997; Strik, 2005; Debersaques *et al.*, 2014) while others have reported self-infertility (Williams *et al.*, 2003) and fruit formation *via* parthenocarpy (Mizugami *et al.*, 2007).

Monet *et al.* (1997) and Hirsch *et al.* (2001) obtained hybrid progenies between an Issai selection of Aa and some male parents of Ad through the *in vitro* rescue of embryos in the torpedo state. However, it is still unknown to the present whether these interspecific hybrids could be obtained through controlled crosses without resorting to interspecific embryo rescue.

This article reports on the progress made in the first steps of obtaining potential hybrid rootstocks. The aim of these steps was to generate interspecific hybrids by conventional hybridization between an Issai selection of Aa and different male genotypes of Ad, without rescuing embryos. Besides that, the effects of the male genotype on seed set and percentage of normal seedlings as well as the variation in hybrid root traits were evaluated in order to identify the genotypes with potential for exploitation in rootstock breeding programs.

Materials and methods

Plant material: An hexaploid selection of Issai of Aa available at the Dalpane nursery in Argentina was used as female parent while four hexaploid cultivars (clones) of Ad (Summerfaenza®, Chieftain, M52 and M56) as male parents. All materials were grown in Southeastern Buenos Aires, which represents the most productive kiwifruit area in Argentina.

Controlled crosses: To check whether the Issai selection available in this study was self-fertile, anthers were removed at flowering to indirectly estimate pollen viability by observing – under a light microscope- pollen sample stained as described by Peterson *et al.* (2010), and unpollinated flowers were covered with paper bags before flowering in order to evaluate fruit formation by parthenocarpy.

To perform the controlled crosses, the flower buds of Issai selection were bagged before anthesis and then hand-pollinated with pollen of four male cultivars, generating four hybrid families. Because Issai selection is more precocious in flowering than some male cultivars used in this study, pollen of each of them was collected the previous flowering season, stored at -20°C for about one year and used when fresh pollen was not enough or available. Fruits were harvested 90 days after pollination. Fruit weight and seed number per fruit were recorded to evaluate the male parent's effect on these traits.

Obtaining hybrid seedlings: Seeds were extracted from fruits and scarified with an abrasive paper. They were disinfected with sodium hypochlorite (20 % commercial bleach water) for 10 minutes and 70 % alcohol for 15 seconds, rinsing with sterile

distilled water after treatments. Then, they were stratified in absorbent paper moistened with distilled water at 4°C for 30 days, and immersed in 2,500 ppm gibberellic acid solution for 24 h. Afterward, seeds were washed with sterile distilled water, left to dry for 24 hours and then sown. To evaluate the effect of the male parent on germination variables, an assay with a completely randomized design with four repetitions was carried out. Seeds (50 per experimental unit) were placed on sterile paper napkins moistened with sterile water. The napkins were rolled up, placed in plastic bags and incubated in the dark at constant 23°C. The data for each hybrid family recorded were: 1) percentage of germination (it was considered to have occurred when the radicle had emerged 2mm), 2) mean germination time according to Edmond and Drapala (1958), 3) percentage of normal seedlings (those that presented the expanded cotyledons and did not present necrosis or defects in hypocotyl and radicle). Data were subjected to one-way ANOVA. Statistical differences at $P \leq 0.05$ were considered significant, and means were compared with LSD test using the R package (R Development Core Team, 2014).

Normal seedlings were transplanted into individual plastic black pots of 7 cm diameter, filled with a mixture of peat and perlite (8:2) and transferred to a growth chamber at 24°C, receiving an average luminous intensity of 140 $\mu\text{mol PAR photons m}^{-2} \text{s}^{-1}$ and watered with half-strength Hoagland's solution. Seedlings were morphologically compared with their parents. Roots were washed and analyzed using a scanner Epson XL10000 and the WhinRHIZO Pro2004a software (Regent Instruments, Canada).

Results

Controlled crosses: All the pollen grains of the Issai selection were non-viable. It is consistent with the presence of shrunken pollen grains of abnormal appearance with little cytoplasm, as shown in Fig. 1. These results indicated that the Issai selection used in crosses as a female parent was totally male sterile, which was of great practical importance when controlled crosses were made due to the fact that emasculation is labour-intensive and time-consuming. In line with the results obtained by Mizugami *et al.* (2007), seedless fruits from unpollinated flowers were obtained. They were smaller than those obtained by artificial pollination (3.5 vs 6.5 g on average). These findings demonstrate that the Issai selection available in this work is not self-fertile but can produce fruits parthenocarpically.

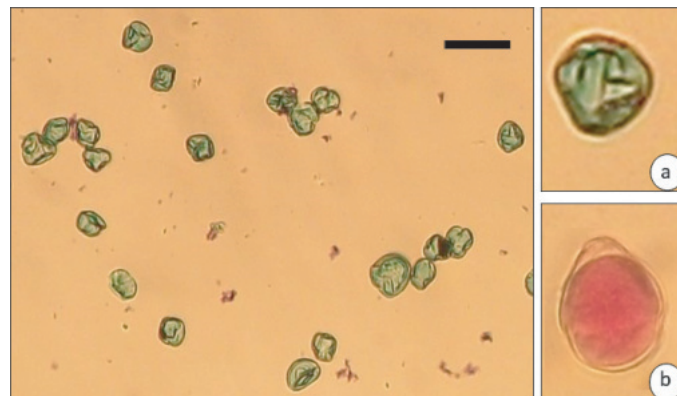


Fig. 1. Aborted pollen grains of Issai selection (*A. arguta*). Scale bar: 100 μm . (Magnified views of aborted (a) and non-aborted (b) pollen grains are included for comparison)

Conventional intraploid crosses were performed, yielding fruits with seeds in all four interspecific genotypic combinations. Fruit weight varied from 3.6 to 12.9 g, whereas seed number per fruit ranked between 8 and 61 (Table 1). The seed set correlated positively with fruit weight ($r=0.845$). This value was similar to the one found in the cultivar Hayward of Ad (Hopping, 1990). Interestingly, fruits resulting from pollination with fresh and stored pollen of male parents were similar in weight and seed set ($P>0.05$). This result is very useful in kiwifruit since some male parents flower later in the season than female parents.

Statistically significant effects of the male parent were found on fruit weight and seed number per fruit (Table 1). Summerfaenza and M52 male cultivars ranked very high for both traits (Table 1). The effect of the pollen source on the development of seed tissues (Xenia) or fruit tissues (Metaxenia) has been found in many fruit crops such as blueberries (Ehlenfeldt, 2003), apples (Militaru *et al.*, 2015), grapes (Sabir, 2015) and sour cherries (Ansari *et al.*, 2010). In kiwifruit, male parent effects were found on number, weight, firmness, soluble solids content, shape and dimensions of fruits in Ad (Qj *et al.*, 2007), fruit flesh colour in Ach (Seal *et al.*, 2013) and fruit total phenolic concentration and seed protein profile in Aa (Stasiak *et al.*, 2019).

Table 1. Effect of male parent on fruit weight and seed set

Male parent	Fruit weight (g)		Seed number/fruit	
	Mean	Range	Mean	Range
Summerfaenza	7.79 a	4.5-12.9	34 a	13-61
M52	7.62 a	5.0-9.6	28 ab	19-42
Chieftain	6.14 b	3.9-8.5	24 bc	18-30
M56	5.07 b	3.8-5.7	19 c	8-30
P-value	<0.0001		0.0002	
CV, %	25.6		36.5	

Means with different letters in a column are significantly different ($P\leq 0.05$)

Obtaining hybrid seedlings: Statistically significant effects of the male parent were found on the percentage of germination and the percentage of normal hybrid seedlings (Table 2). Pollination with Chieftain pollen yielded the lowest percentage of seeds with normal constitution (teguments, embryo and endosperm with normal appearance) and the lowest proportion of normal hybrid seedlings (Table 2). Most abnormal seedlings produced on the germination test were characterized by being twisted and having their cotyledons held within the seed coats (Fig. 2a), whereas a few seedlings showed aberrant growth at more advanced stages (Fig. 2b).

Table 2. Effect of male parent on percentage of germination and normal hybrid seedlings

Male parent	Germination (%)	Mean germination time (days)	Normal seedlings (%)
Summerfaenza	38.00 ab	13.99 a	23.20 a
M52	34.00 ab	12.67 a	12.00 bc
Chieftain	29.60 b	13.60 a	3.20 c
M56	44.00 a	12.97 a	12.66 b
P-value	0.00039	0.77	0.0075
CV(%)	23	7.87	73

Means with different letters in a column are significantly different ($P\leq 0.05$)



Fig. 2. Abnormal interspecific seedlings (a) during germination test and (b) three weeks after germination

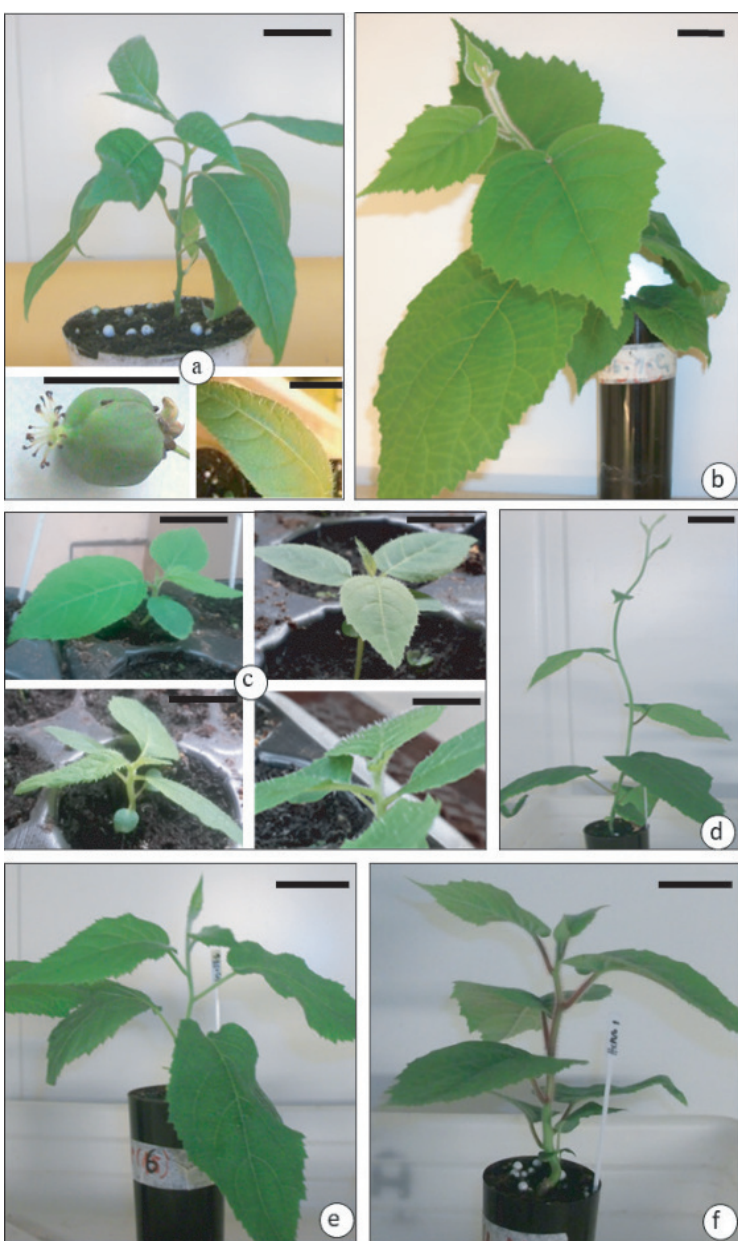


Fig. 3. Plant morphology of interspecific hybrids and their parental species. (a) *A. arguta* (Issai selection) showing leaves and fruit, (b) *A. chinensis* var. *deliciosa* (Hayward x M56), (c) two-week-old interspecific seedlings, (d-f) six-week-old interspecific seedlings from crosses (d) Issai x Summerfaenza, (e) Issai x M52 and (f) Issai x M56. Scale bar=5cm

Normal seedlings continued their growth and showed intermediate phenotypes compared to both their parents (Fig. 3). It is worth noting that each plant is a unique genotype due to the high heterozygosity of its parents (Liu *et al.*, 2015). Variations in aerial morphological characters such as leaf margin type, leaf shape (length/width) and hair density on leaf, stem and petiole were observed (Fig. 3). A wide variation in root architecture characteristics such as total length, surface area, volume, average diameter and dry weight was also detected among the hybrid progenies (Table 3 and Fig. 4) identifying hybrids with less vigorous root systems than those of *A. chinensis* var *deliciosa*.

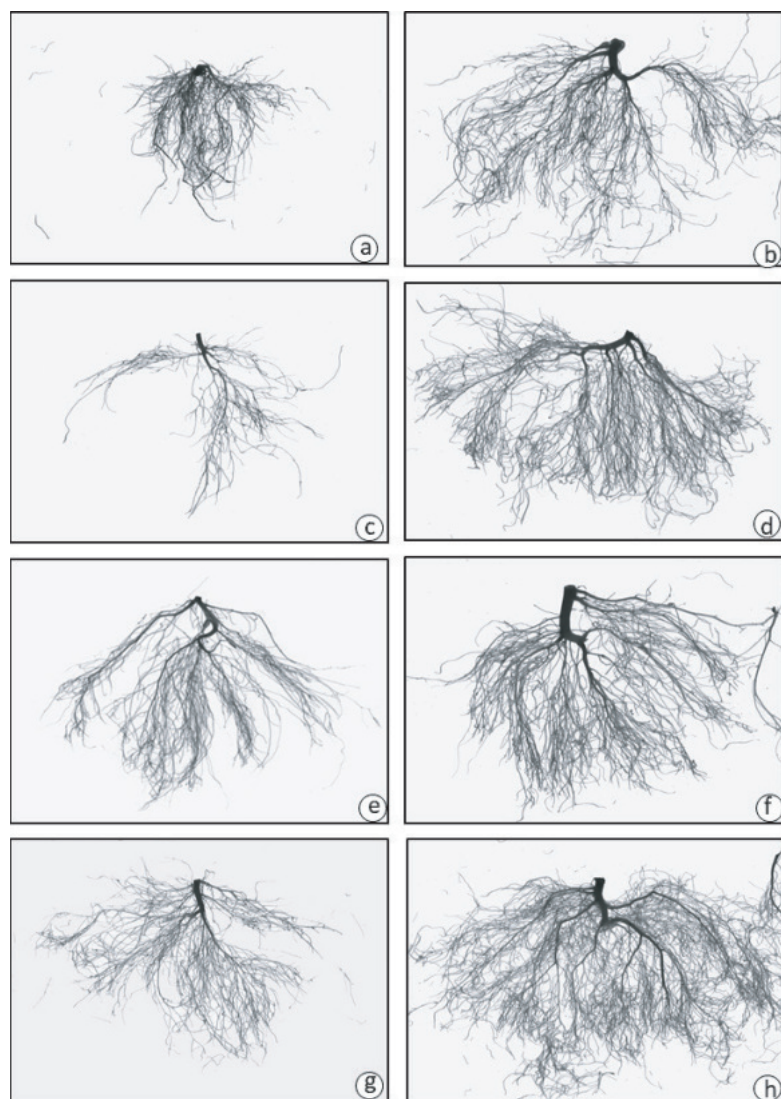


Fig. 4. Root systems of interspecific hybrids and their parental species. (a) *A. arguta* (Issai selection), (b) *A. chinensis* var. *deliciosa* (Hayward x M52), (c-h) interspecific seedlings from crosses (c-d) Issai x M52, (e-f) Issai x M56, (g-h) Issai x Summerfaenza. All images are at the same magnification

Table 3. Root characteristics of interspecific hybrids and their parental species

Root characteristics	Parental species		Interspecific hybrids ³
	<i>A. arguta</i> Issai selection ¹	<i>A. chinensis</i> var. <i>deliciosa</i> ²	
Total volume (cm ³)	0.855	4.34	2.19
Total surface area (cm ²)	63	284.3	166.6
Total length (cm)	369.4	1497.9	1064.4
Average diameter (cm)	0.54	0.59	0.52
Dry weight (g)	0.049	0.365	0.154

¹ one genotype. ²average of six genotypes. ³average of 18 genotypes

Discussion

Interspecific hybridization is an effective way to create desirable rootstocks that combine favourable traits from different germplasm for the grafting of several fruit crops (Mudge *et al.*, 2009) and vegetable crops (King *et al.*, 2010). Through grafting, two plant parts (rootstock and scion) are fusionated so that vascular continuity is established between them and the resulting genetically composite organism functions as a single plant. This is a highly effective environmentally-friendly technique not only to reduce losses in production caused by biotic and abiotic stress conditions but also to control plant size and increase fruit quality and yield (Mudge *et al.*, 2009; Lee *et al.*, 2010; Schwarz *et al.*, 2010).

There are several examples of intergeneric and interspecific hybrids successfully used as rootstocks for the grafting of vegetable and fruit crops such as *Solanum lycopersicon* x *S. habrochaites* for tomato, *S. integrifolium* x *S. saniwongsei* for eggplant, *Cucurbita maxima* x *C. moschata* for watermelon and melon (King *et al.*, 2010 and Lee *et al.*, 2010), *Prunus cerasifera* x *P. munsoniana* for apricot (Reig *et al.*, 2018), *Citrus spp.* x *Poncirus trifoliata* for Citrus trees (Simpson *et al.*, 2015), *Actinidia eriantha* x *A. hemsleyana* (cultivar Kaimai) for kiwifruit (Wang *et al.*, 1994; Huang, 2016). Analogously, Aa x Ad hybrids with reduced root area would be used as rootstocks for kiwifruit vines in order to control the vegetative growth.

Some of the aforementioned intergeneric or interspecific hybrids could not be obtained by conventional crosses due to crossing barriers. Therefore, manipulations tending to circumvent barriers such as embryo culture and somatic hybridization needed to be carried out (Guo *et al.*, 2002; Karaağaç and Balkaya, 2013). According to Hadley and Openshaw (1980), there may be two types of internal hybridization barriers operating between two species: pre-zygotic -acting at the pollen-stigma or pollen-style levels- and post-zygotic, acting at the endosperm, embryo or even in the F₁ generation or in more advanced segregating generations. In *Actinidia*, Hirsch *et al.* (2001) obtained interspecific hybrids through embryo rescue from inter- and intra-ploid crosses, including Aa and Ad at hexaploid level.

In our study, besides the empty seeds and abnormal hybrid seedlings at different stages (Fig. 2), the maximum number of seeds obtained per fruit (61 in Table 1) was low if the fact that intraspecific intraploid crosses of Aa produced up to 266 seeds is considered (Mizugami *et al.*, 2007). This was interpreted to mean that incomplete hybridization barriers are operating between Ad and Aa. Notwithstanding that, normal progenies in all the four genotypic combinations were obtained without rescuing *in vitro* embryos.

Interspecific hybrids showed useful variability in root traits within and between families. In this context, it is advisable to consider the male parent effects on percentage of germination and normal hybrid seedlings

for the breeder to have the genetic variability necessary to make an efficient selection of the genotypes with less vigorous root systems. It is worth mentioned that these promising individuals must be evaluated in the future for their effects on the scion and their affinity as rootstocks.

It has been demonstrated in this investigation that the intraploid hybridization between Aa and Ad produces normal progenies, at least in the four genotypic combinations, without rescuing *in vitro* embryos, and that these hybrids vary in the degree of root system vigor. The finding that root systems in many interspecific hybrids are less vigorous than those in Ad further highlights the potential of the intraploid hybridization between these species to develop rootstocks with size-controlling potential. It is important to note that rootstocks that have reduced root area represent a better option than root pruning because the later approach is quite invasive to the plant (Black *et al.*, 2012). Moreover, it must be emphasized that no root system has ever been showed in interspecific crosses of *Actinidia*, being this study the first in doing so.

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