

November 2000

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Adaptive Response of *Scaphyglottis acostaei* (Orchidaceae) to Microhabitat Variability

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ABSTRACT

Orchids exhibit many adaptations, including pseudobulbs which store water and root velamen, which assists in water uptake, to deal with the harsh, water stressed conditions that are an integral part of epiphytic life. Within a single host tree the intensity of water stress varies between microhabitats caused by presence of moss and bark fissures to reduce evaporation of water, and positions that increase or decrease exposure to wind, precipitation and sun. The orchid, *Scaphyglottis acostaei* exhibits variable pseudobulb sizes and water holding potential of velamen, possibly as a result of different levels of water stress and water availability. In this study I compared water holding capacity of the velamen and average size of pseudobulbs between individuals in different microhabitats. It was found that the presence of moss was associated with an increase in the water holding potential of velamen and decreased the average size of pseudobulbs. There was a positive correlation between the dry weight of velamen and the amount of water it can hold, indicating a increased production of velamen with greater water ability. This increase in velamen production could be a result of the potential to absorb more water in areas where it is more available. The decrease in pseudobulb size when water is more abundant is attributed to the reduced need for storing water.

RESUMEN

Orquídeas (Orchidaceae) presenta muchas adaptaciones, incluyendo seudobulbos, por depósito de agua y velamen por el contacto prolongado con agua y asiste el colección de agua por la ambiente severa y estrés de agua que se supone es la vida en los arboles, epifitas. En un arbol singular hay mucho variación del estrés de agua entre los micro-hábitats. Este es un resultado de la presencia de musgo y las grietas de la corteza reducir el evaporación del agua y posiciones que incrementar o reducir exposición al viento, la llueve y el sol. El orquídea, *Scaphyglottis acostaei* es un especie de Orchidaceae que presenta un tamaño variable del seudobulbos y posesión de agua en el velamen de los raíces. Es posible que este es un resultado de variable en el estrés de agua. En este estudio comparo el capacidad para el velamen de agarrar agua y el tamaño promedio del seudobulbos en micro-hábitats diferentes. Encontre que mas presencia de agua, la presencia del musgo, incremente la capacidad del velamen de agarrar agua y reducir el tamaño promedio del serudobulbos. También había una correlación positiva entremedias el peso seco del velamen y el peso del agua en el velamen después de remojo. Es posible que este incremento en la inversión de velamen es un resultado del potencial de absorber mas agua cuando esta está más disponible. La disminución en la inversión de velamen es un resultado del potencial de absorber mas agua cuando esta mas disponible. La disminución en el tamaño de seudobulbos cuando agua está más disponible es un resultado de que el reduce la necesidad por agarrando agua.

INTRODUCTION

Tropical forests exhibit great variability in ranges of temperature, humidity, light and wind intensity between the upper and lower strata of the Forest (Richards 1996).

Although, in cases where human activity has disturbed the original structure of the forest, as in pastures, the micro-climatic variability and intensity characteristic of the upper strata is felt at all levels (Johansson 1974).

This has enormous implications for epiphytic orchids living on trees in pastures, most importantly in respect to water availability. Vertically stratified zones that correspond to varying amounts of sun, wind and moisture have been identified within host trees (Johansson 1974). This variation creates numerous, subtly different microhabitats within a given tree. Within these zones the shape of the tree and branching pattern create numerous sites, such as crevices where climatic variables are either intensified or reduced. Compass orientation zones also create variation in a plant's exposure to the drying forces of wind and amount of precipitation captured from wind driven rain and mist.

Heterogeneity in the physical properties of the bark and presence of other epiphytes also contribute importantly to microhabitat variation within and among host trees. Next to the presence of organic humus, mosses and other moisture-retaining epiphytes are probably the most important factor for regulating the availability of moisture for epiphytic orchids (Benzing pers. comm.). Fissured bark may (why do I have to say this) also contribute to water absorption and retention.

Due to the transient nature of water in tree tops, epiphytes must be able to absorb water quickly when it is available and not lose it too fast when it is not (Richards 1981). The water-stressed nature of the epiphytic growth form has led to numerous adaptations for the conservation of water (Benzing 1995). Epiphytic orchids show incredible diversity in the combination of traits such as pseudobulbs and velamen that allow them to tolerate a degree of water stress that would damage most other plants (Dressler 1990).

Velamen is made up of dead, hollow cells with thin walls, surrounding the entire length of the root (Figure 1). It services the plant primarily by prolonging contact with precipitation and secondarily by redrawing loss of water (Benzing and Atwood 1984). There may be between two and 18 layers of cells in the velamen of any given orchid (Dressler 1990). Alternatively, pseudobulbs allow for the long-term storage of water, to be drawn upon in times of water scarcity. They are commonly found in species in which the old stem ceases to grow in length and instead, exhibits secondary thickening at one or several nodes.

Scaphyglottis acostaei, an orchid of the subtribe Laeliinae, exhibits a mat-like growth form with many shoots of thin stems that form thin, narrow, elliptical pseudobulbs that vary in size within and between mats. This study seeks to shed some

light onto the variation in size of pseudobulbs as well as thickness and water holding capacity of velamen among individuals. I hypothesize that this variation is due to the degree of water stress that a plant experiences between microhabitats on host trees. In microhabitats where water stress is greater plants should invest more heavily in pseudobulbs due to a heavier reliance on water storage in times of stress. Additionally, because velamen prolongs contact with precipitation an increase in the availability of moisture should be accompanied by heavier investment in velamen to better take advantage of the favorable conditions. Finally, I expect that relative investments in velamen and pseudobulbs to be negatively correlated with each other, increased investment in one should lead to reduced investments in the other. In building velamen, the plant may sacrifice living root tissue to the task of collecting water and replace that layer with a new layer of living root-cells. Therefore, in stressful environments, production of additional velamen costs the plant enough energy, seen in the building of new root tissue, that it must compromise other systems.

METHODS

Study site

This study was conducted between October 20 and November 15 of 2000 in the pasture located just North of La Estación Biológica, Monteverde, Costa Rica. The 2.5 ha pasture is surrounded by Lower Montane Wet Forest at an altitude of between 1500m and 1600m. The climate is characterized by three seasons: (1) a wet season that lasts from approximately May through October (2) a “rainy-misty” season when strong, northeasterly trade winds bring mist and horizontal rain from November until January and (3) a dry season from February to April with mist usually at night (Clark et al. 2000).

Pseudobulb and Velamen Characteristics

Mats of *S. acostaei* were considered separate individuals to reduce the chance of sampling genetically identical plants. Individuals with at least 10 pseudobulbs were sampled on the basis of pseudobulb size and velamen characteristics. Pseudobulb area (length and width) was measured (mm) on five pseudobulbs per individual with digital calipers and then averaged. Approximately 10 roots between three and four cm with intact velamen were taken from the tips of the roots of each individual, placed in plastic zip-lock bags and numbered. In the lab the velamen was separated from the roots with forceps. All roots and velamen for each individual were weighed together on a Fisher Scientific XT top loading digital balance and then placed in a drying oven with a 75 watt incandescent bulb for 19 hours. The following day the roots and velamen were weighed again and then submerged in water for 30 minutes. After draining, using perforated filter paper, the roots and velamen were dabbed with tissue paper to remove excess surface

water and weighed again. These soaked weights were used to calculate both the weight of water (soaked wt. – dry wt.) and the WHP (water holding potential) for velamen and roots by the formula: (soaked wt – dry wt)/dry wt. The velamen: root weight ratio was also taken by dividing the dry weight of velamen by dividing the dry weight of velamen by the dry weight of root.

Microhabitat Conditions

Johanson's (1974) model of epiphytic zonation on West African rain forest trees was followed in assigning zones to pasture trees (Figure 2). Zones two, three and four were sampled. The more inaccessible individuals in all three zones were sampled with the use of a ladder and occasionally free-climbing. *Scaphyglottis acostaei* individuals were not found in zone one, and were inaccessible in zone five.

Bark texture was categorized in terms of the presence or absence of fissures. Moss was evaluated solely on its presence or absence. The position of each individual on the tree was also noted by recording whether the orchid was in a vertical or horizontal position and if it was situated in a crevice or lay flush against the tree.

The host trees were divided into four compass quadrants (north to east, north to west, west to south and south to east), and the position of each individual *S. acostaei* was recorded.

Statistical Analyses

Kruskal-Wallis tests were used to determine if average pseudobulb area, the velamen: root weight ratio, and the WHP of velamen were affected by zone and compass quadrant. Mann-Whitney U tests were used to determine if the position, exposure (crevice or flush), and the presence or absence of fissures and moss were related to pseudobulb size, velamen: root weight ratio and WHP of velamen. Three simple linear regressions were performed comparing the water weight of velamen vs. dry weight of velamen, average pseudobulb area vs. velamen: root weight ratio and average pseudobulb area vs. WHP of velamen. Normality tests were performed on the three variables for the regressions. In order to achieve normality in velamen: root weight ratio and the WHP of velamen it was necessary to use natural log-transformed values.

RESULTS

I sampled 49 *S. acostaei* on 15 pasture trees of unknown species. None of the Kruskal-Wallis tests showed a significant effect of zone or compass quadrant on average pseudobulb size, velamen: root weight ratio or the WHP of velamen (Tables 1-2).

One of the Mann-Whitney U tests showed a significant effect of moss presence on average pseudobulb area ($P = 0.0328$, $U = 199.0$; see Table 3 and Figure 3). The presence or absence of moss also showed a near significant effect on the velamen: root weight

ratio ($P = 0.0546$, $U = 192.0$; see Table 3 and Figure 4). The rest of the Mann-Whitney U tests did not show significant differences (Table 4-6).

Of the three regressions performed only one showed significance (Figures 5-8). The weight of water in velamen was positively correlated with the dry weight of velamen ($P < 0.0001$, $R = 0.606$, $F = 27.325$, Figure 5).

DISCUSSION

In *S. acostaei*, heavier velamen holds more water than lighter velamen as indicated by the positive correlation between water weight in velamen and the velamen dry weight (Figure 5). Heavier velamen is due to increased investment by the plant adding layers of porous cells to the velamen. All things being equal, the longer the contact with precipitation, the thicker the layer of velamen corresponding to greater investment made by the plant (Benzing pers. comm.).

This can also be seen in the effects of moss and bark fissures on the velamen: root ratio and the WHP of velamen respectively. The presence of moss showed a near significant effect on the velamen: root weight ratio (Figure 4, Table 3). An increase in the weight of velamen relative to the weight of roots in the presence of moss illustrates that more velamen is produced to take advantage of the greater availability of moisture in beds of moss. The strength of this relationship is reflected in the small sample size of individuals growing in the absence of moss.

Although the difference was not significant, a slight increase in the WHP of the velamen was seen on trees with fissured bark. The greater water holding capacity of fissured bark may allow *S. acostaei* to more heavily invest in velamen, in order to prolong contact with available moisture.

The effect of moss on the physiology and morphology of *S. acostaei* can also be seen in the average sizes of pseudobulbs. Pseudobulbs on plants growing in the absence of moss were significantly larger than those of plants growing with moss ($P = 0.0328$, Figure 3, Table 6). In areas with little moss to assist in the retention of water, the need to store water is great, and pseudobulbs are correspondingly larger, increasing long-term storage of water.

Benzing (1995) reports that rainfall distribution over the course of the year is more closely linked to epiphyte success than total annual rainfall. During the dry season, when precipitation is intermittent moisture can remain trapped in beds of moss, effectively shortening the length of these dry spells. In wetter habitats the presence of other epiphytes is probably important in making long-term moisture availability more constant thereby enhancing the success of orchids. In *S. acostaei* and possibly orchids in general, reduced water stress decreases the plants dependence on long-term storage as seen in the reduced mean size of pseudobulbs in the presence of moss. However, both investment and thickness of velamen increases with added moisture. This is probably a result of the

different primary functions of velamen and pseudobulbs; long-term storage and prolonging contact with precipitation.

The unexpected results of the two regressions comparing WHP, average pseudobulb size and velamen: root ratio may be explained by the relative cost of velamen versus pseudobulbs. One would expect that if both structures were expensive for the plant to produce there would be a trade off in the abundance or relative sizes of each. Larger investment in Velamen would mean a reduced investment in pseudobulbs and the reverse. It was found however that they did not correlate at all (Figures 6-8). Velamen is relatively cheap to produce and maintain at maturity because it is comprised of dead thin walled cells. The pseudobulb on the other hand, is more costly as it contains living cells at maturity, some of which contain chloroplasts which are very expensive relatively (Benzing pers. comm.). Additionally, because the two structures differ in their primary functions it is not really valid to expect them to correlate in any way.

Considering the morphology and physiology of the leaves with respect to microhabitat conditions in comparison to pseudobulb characteristics could produce some interesting insights into water conservation strategies of *S. acostaei*. Chicurel (2000) found that the percent water content of leaves of *S. acostaei* was negatively correlated with thickness. Leaf age was hypothesized to be the cause of this counter-intuitive result. *S. acostaei* showed the greatest mean stomatal density and lowest water content of any of the six species of orchids observed. *Scaphyglottis acostaei* fixes CO₂ via the C₃ pathway and so this increase in stomatal density over other CAM plants is expected (Benzing pers. comm.). In order to better conserve water and complement pseudobulb storage, I hypothesize that with increasing water stress the water content of the leaves would increase with a corresponding decrease in stomatal density.

Epiphytic orchids can effectively conserve water using different strategies involving different anatomical and physiological traits with the similar efficiency. It is hard to use a few morphological characteristics of an orchid to interpret its response to climatic and substrate variability between habitats (Benzing, pers. comm.). Microhabitat heterogeneity is so great and dependant on so many different characteristics that it is also extremely hard to evaluate it on the basis of only a few select variables. Measurements such as wind speed, light intensity and quantitative measurements of moisture availability may assist in accurately describing microhabitat variability. Despite small sample sizes and incomplete measures of microhabitat variability, this study does provide some insight into the effects of water stress on morphology of orchids in different microhabitats. As with many studies of orchids in the neo-tropics, the need for further investigation is apparent.

ACKNOWLEDGMENTS

The greatest and most endearing thanks to Karen Masters for her unending assistance in helping me design a project, redesign my project, answering my questions, explaining statistics in exactly the right way, prodding me to think and putting up with my non-linear brain! Enormous thanks to two of the most helpful TA's ever, Andrew Rodstrom and Timothy Kuhman for staying up late reading all of our papers and running back and forth to the cabinets for me. This study would not have been possible without the use of Arnoldo Beche's beautiful pasture. My understanding of vascular epiphytes has been advanced enormously by the expertise of my advisor Dr. David H. Benzing. Also to Mauricio Garcia, and Alan Masters for answering my questions when Karen wasn't around and for giving me laughs. Oh, and the cooks for keeping us fed.

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Table 1. Values for Kruskal-Wallis tests for the effect of compass quadrant on the velamen:root weight ratio, the average pseudobulb area and the velamen WHP. Differences between means of the four populations were not significant

		Velamen:Root wt. ratio	Average Pseudobulb Area	Valamen WHP
CQ		X (SE) n	X (SE) n	X (SE) n
	NE	3.934 (0.387) 16	104.67 (5.56) 16	2.919 (0.234) 16
	SE	4.087 (0.363) 13	104.38 (5.85) 13	2.595 (0.209) 13
	SW	3.402 (0.299) 11	96.50 (5.57) 11	2.791 (0.023) 11
	NW	4.993 (1.072) 9	95.59 (4.52) 9	3.009 (0.310) 9
		P = 0.3671 H = 3.164	P = 0.4843 H = 2.450	P = 0.6674 H = 1.565

Table 2. Values for Kruskal-Wallis tests for the effect of tree zone on the velamen:root weight ratio, the average pseudobulb area and the velamen WHP. Differences between means of the three populations were not significant

		Velamen:Root wt. ratio	Average Pseudobulb Area	Valamen WHP
Zone		X (SE) n	X (SE) n	X (SE) n
	2	3.775 (0.229) 20	108.52 (4.81) 20	2.792 (0.178) 20
	3	4.282 (1.647) 16	95.99 (3.35) 16	2.974 (0.256) 16
	4	4.224 (0.498) 13	95.80 (5.51) 13	2.677 (0.182) 13
		P = 0.8492 H = 0.327	P = 0.1977 H = 3.242	P = 0.8688 H = 0.281

Table 3. Mann-Whitney U test results for the effect of the presence of moss on the velamen:root weight ratio, the average pseudobulb area and the velamen WHP. Significance is seen in the effect of moss on the velamen:root weight ratio and the average pseudobulb area.

		Velamen:Root wt. ratio	Average Pseudobulb Area	Valamen WHP
Moss		X (SE) n	X (SE) n	X (SE) n
	Presence	4.202 (0.172) 43	98.49 (2.751) 43	2.842 (0.85) 43
	Absence	3.038 (0.292) 6	119.42 (8.391) 6	2.668 (0.777) 6
		P = 0.0546 U = 192.00	P = 0.0328 U = 199.00	P = 0.6917 U = 142.00

Table 4. Mann-Whitney U test results for the effect of position on the velamen:root weight ratio, the average pseudobulb area and the velamen WHP. The effect was found to not be significant on the selected variables.

		Velamen:Root wt. ratio	Average Pseudobulb Area	Valamen WHP
Position		X (SE) n	X (SE) n	X (SE) n
	Vertical	4.101 (0.303) 39	100.60 (3.33) 39	2.752 (0.126) 39
	Horizontal	3.900 (0.530) 10	102.82 (4.15) 10	3.091 (0.351) 10
		P = 0.7098 U = 210.00	P = 0.6914 U = 211.00	P = 0.4129 U = 228.00

Table 5. Mann-Whitney U test results for the effect of exposure on the velamen:root weight ratio, the average pseudobulb area and the velamen WHP. The effect was found to not be significant on the selected variables.

Exposure	Velamen:Root wt. ratio	Average Pseudobulb Area	Valamen WHP
	X (SE) n	X (SE) n	X (SE) n
Crevice	3.799 (0.392) 12	107.12 (4.85) 12	2.938 (0.249) 12
Flush	4.144 (0.325) 37	99.08 (3.29) 37	2.783 (0.137) 37
	P = 0.6586 U = 241.00	P = 0.2010 U = 277.00	P = 0.5225 U = 249.50

Table 6. Mann-Whitney U test results for the effect of the presence of bark fissure on the velamen:root weight ratio, the average pseudobulb area and the velamen WHP. An interesting trend is seen in the mean values for WHP in the presence and absence of bark fissures that suggests *S acostaei* makes heavier investment in valmen when more moisture is available.

Bark Fissure	Velamen:Root wt. ratio	Average Pseudobulb Area	Valamen WHP
	X (SE) n	X (SE) n	X (SE) n
Presence	4.392 (0.537) 21	99.83 (3.57) 21	30.69 (0.209) 21
Absence	3.810 (0.220) 28	101.97 (4.10) 28	2.635 (0.131) 28
	P = 0.6713 U = 315.00	P = 0.6278 U = 318.00	P = 0.0996 U = 375.50

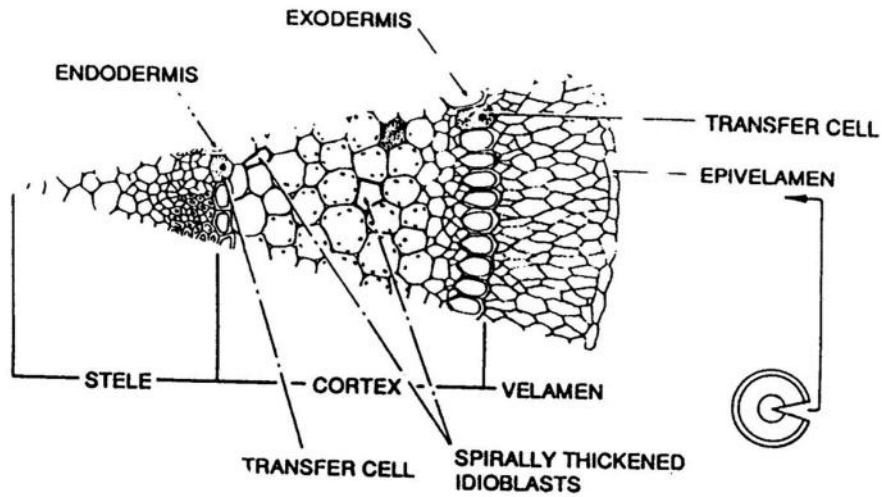


Figure 1. Diagram of a section through a typical orchidaceous root showing the position of the velamen and exodermis. From Benzing (1995).

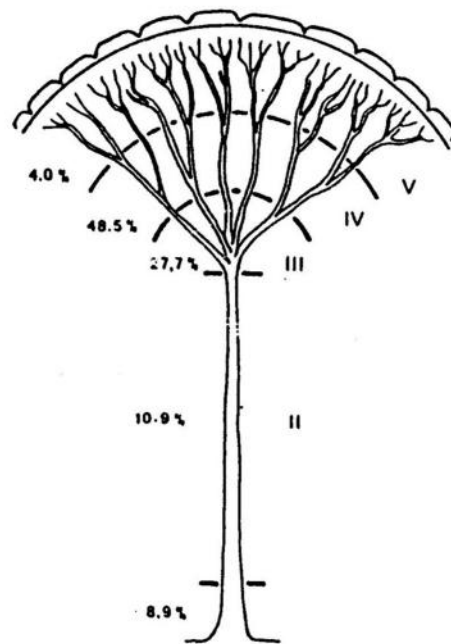


Figure 2. Tree zones according to Johansson (1974) for epiphytic orchid distribution in host trees of a West African rainforest.

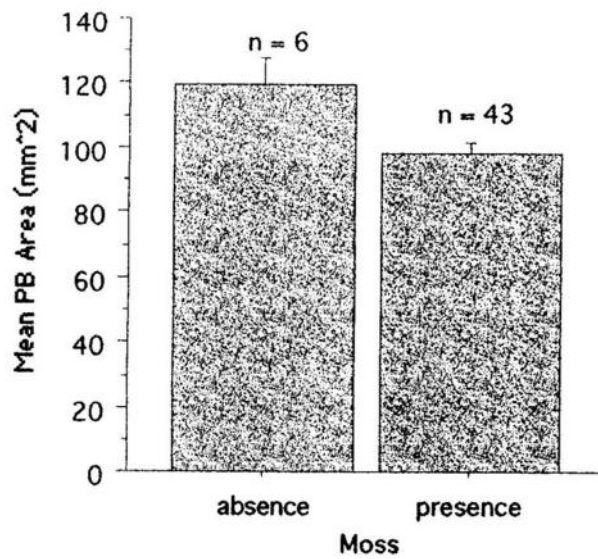


Figure 3. The effect of moss presence on the average pseudobulb area. There was a significant ($P = 0.0328$, Mann Whitney U test) increase in the average pseudobulb area on individuals growing without moss. The small sample sizes emphasize the significance of this effect.

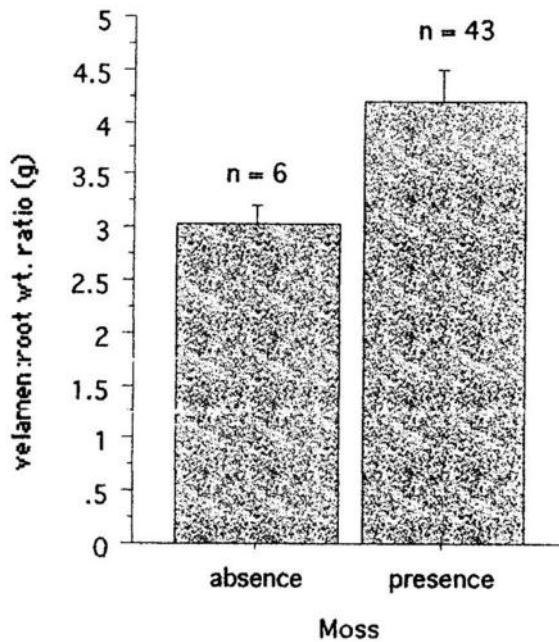


Figure 4. The effect of moss presence on the velamen:root weight ratio. There was a near significant ($P = 0.0546$, Mann Whitney U test) increase in the relative investment in velamen compared to roots in individuals growing with moss. With increased sample sizes, it is expected that significance will increase.

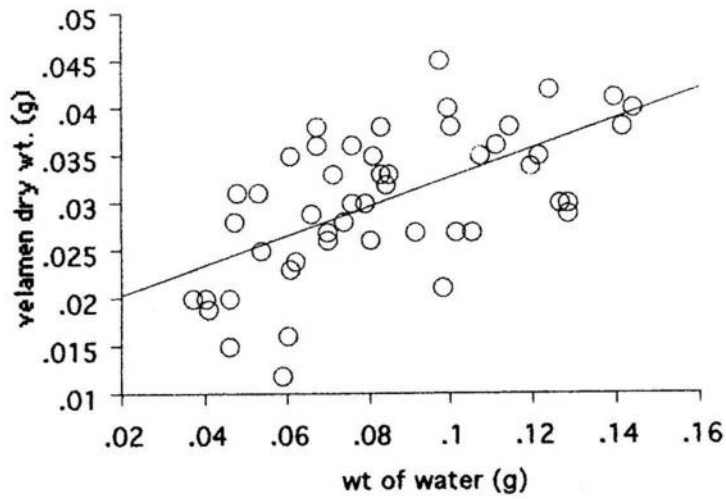


FIGURE 5. A Simple Linear Regression showed that the weight of water in velamen was significantly positively correlated with the dry weight of velamen ($P = <0.0001$, $R = 0.606$, $F = 27.325$), indicating that heavier velamen holds more water.

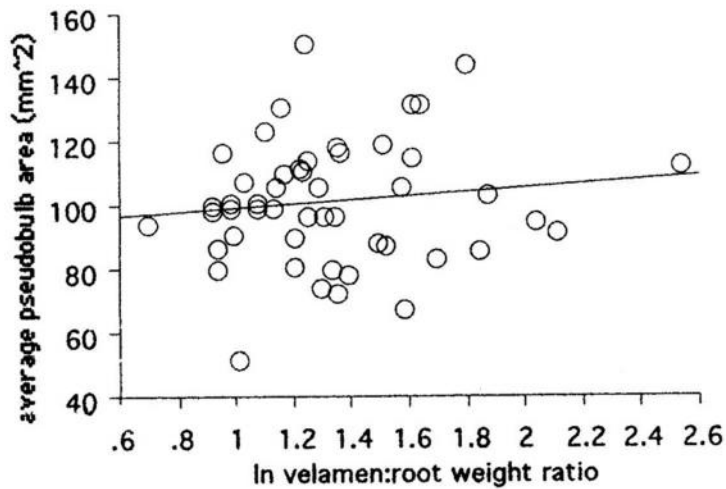


FIGURE 6. A Simple Linear Regression of the average pseudobulb area vs. the ln-transformed velamen: root weight ratio showed there was no significant correlation between the two variables ($P = 0.4236$, $R = 0.117$, $F = 0.652$).

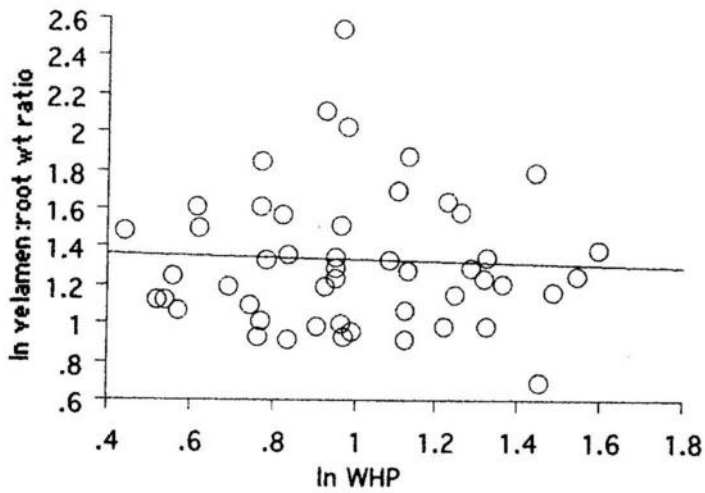


FIGURE 7. A Simple Linear Regression between the ln-transformed values of the velamen:root weight ratio and the WHP (water holding potential) of velamen failed to show a significant correlation ($P = 0.7790$, $R = 0.041$, $F = 0.080$).

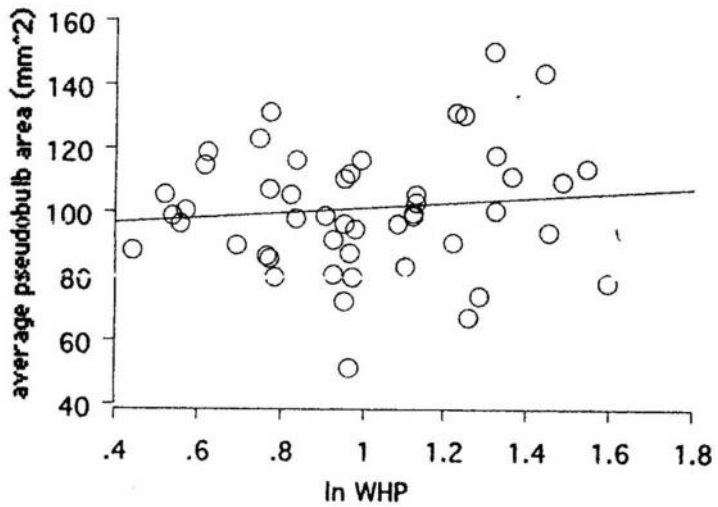


FIGURE 8. A Simple Linear Regression between the average pseudobulb area and the ln-transformed value of the WHP of velamen failed to show a significant effect ($P = 0.4135$, $R = 0.014$, $F = 0.681$).