PETIOLE LENGTH IN *BOERHAVIA* (NYCTAGINACEAE) APPROXIMATES THE GOLDEN RATIO Φ

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ABSTRACT

The leaves of *Boerhavia* exhibit anisophylly. It is here hypothesized that the scale of the uneven leaves exhibits a determined pattern, rather than an arbitrary difference in size. To test for this, the opposite petioles of *Boerhavia diffusa* and *B. erecta* from both regional and local populations were measured, and the ratio of the measurements were compared to the Golden Ratio. One-paired t-tests for a critical mean indicate that the ratios of paired petioles for both species are not statically different from the value 1.6180339887…. These tests indicate that petiole length in *Boerhavia* approximates the Golden Ratio. The significance of this observation is that the Golden Ratio is here expressed as a line segment rather than as a spiral, which is how the Golden Ratio has been previously observed and reported in plant growth.

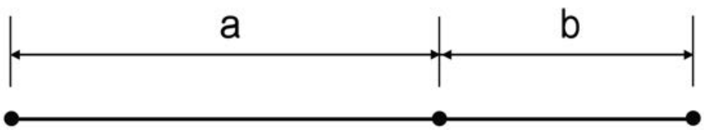
Key Words: *Boerhavia*, Nyctaginaceae, Anisophylly, Anisoclady, C_4, Golden Ratio, phi

RESUMEN

Las hojas de *Boerhavia* presentan anisofilia. Se hipotetiza aquí que la escala desigual de las hojas muestra un patrón determinado, más que una diferencia arbitraria en tamaño. Para probar esto, se midieron los pecíolos opuestos de *Boerhavia diffusa* y *B. erecta* de poblaciones regionales y locales, y las ratios de las medidas se compararon con las ratio medias. Los t-tests de pares para una media crítica indican que las ratios de pares de pecíolos para ambas especies no son estadísticamente diferentes del valor 1.6180339887…. Estos tests indican que la longitud del pecíolo en *Boerhavia* se aproxima a la ratio media. El significado de esta observación es que la ratio media se expresa aquí como un segmento de línea en vez de como una espiral, que es como la ratio media ha sido observada previamente y reportada en el crecimiento de la planta.

INTRODUCTION

The Golden Ratio is an irrational number that has preoccupied mathematicians, artists, and naturalists for millennia. The complex history of the number is demonstrated by the numerous names by which it has been recognized: the Golden Ratio, golden mean, golden section, divine proportion, and by the Greek symbol phi (Φ) (Livio 2003). Euclid (Heath 1956) defined the ratio as a straight line that is cut in extreme and mean ratio when, as the whole line is to the greater segment, so is the greater to the lesser. The following line segment illustrates this definition:



where:

$$\varphi = \frac{a+b}{a} = \frac{a}{b}$$

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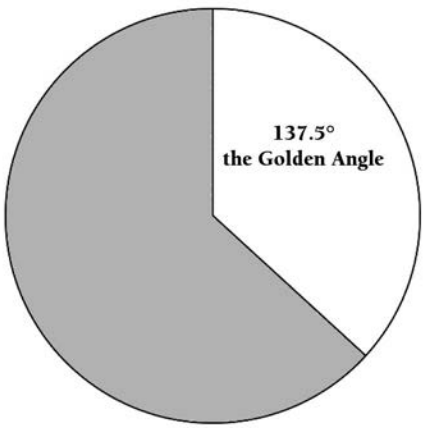
The number itself is determined by the equation:

$$\varphi = \frac{1+\sqrt{5}}{2} = 1.6180339887\ldots$$

The relationship between the Golden Ratio and plant form has been studied extensively. Most specifically researchers have noted that the divergence angle of spirally arranged leaves (Niklas 1988; King et al. 2004), pineapple fruits (Ekern 1968), and florets in sunflower heads (Okabe 2015) is 137.5º, more commonly referred to as the golden angle, where:



$$360º - \left(\frac{360º}{\varphi}\right) \approx 137.5º$$

Two explanations for spiral phyllotaxis following the golden angle have been proposed. The purely mathematical explanation argues that the Golden Ratio is the most efficient means for packing as much material as possible in a given space (Livio 2003). The second explanation is economical; growth patterns exhibiting the Golden Ratio are conserving energy: spiral "phyllotaxis simply represents a state of minimal energy for a system of mutually repelling buds" (Livio 2003).

Boerhavia L. is a genus in the family Nyctaginaceae. The genus is cosmopolitan, growing in deserts and temperate and tropical waste areas throughout the Old and New World. Within the family the genus is readily recognized by its herbaceous habit, anisophylly, and numerous terminal flowers lacking an involucre of bracts. Anisophylly is defined as the asymmetric growth of opposite leaves developing from the same branch node (Fig. 1). As the new leaves develop, the larger leaf of the pair alternates between the left and the right side of the stem so that two large leaves do not develop one after the other on the same side of the stem (Fig. 2). When the plants undergo branching, the branches develop from the nodes of the smaller leaf (Fig. 2). The asymmetric development of lateral branches is termed anisoclady. It is here suggested that the asymmetric leaves of *Boerhavia* "represent a state of minimal energy for… mutually repelling buds" (ibid). It is therefore hypothesized that the growth pattern of the anisophyllous leaves in *Boerhavia* follows the Golden Ratio.

The objective of this paper is to test the hypothesis that "the anisophyllous leaves of *Boerhavia* demonstrate a growth pattern that follows the Golden Ratio."

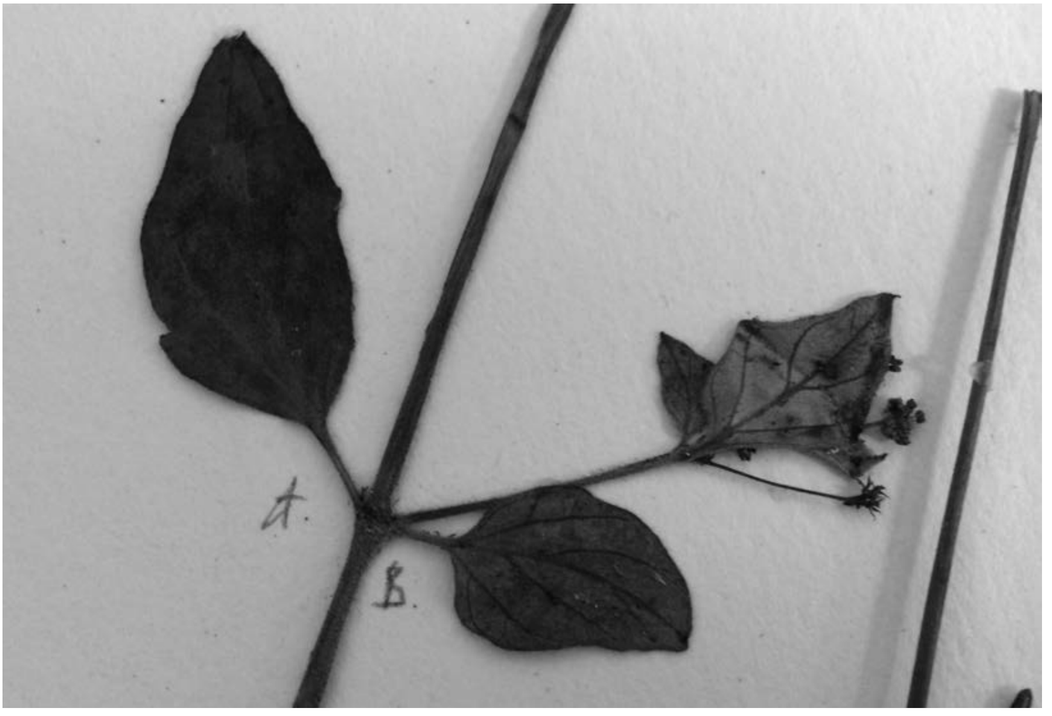


Fig. 1. Opposite pairs of leaves of *Boerhavia diffusa*. Petiole A is the longer petiole, petiole B the shorter. Note branching occurs from the node of the shorter leaf.

METHODS

To test the hypothesis, petiole lengths of opposite pairs of leaves of *Boerhavia* were measured. Both preserved and living material were measured, with measurements coming from herbarium specimens and material collected in the field. Measurements from herbarium specimens represent regional diversity of petiole length, and living material represents the diversity of petiole length within a population. Two different species were measured to identify whether the phenomena occurred across species within the genus *Boerhavia*. Measurements were taken from the base of the leaf blade to the end of the petiole where it meets the stem. Measurements were taken with a digital caliper specific to the nearest 0.01 mm. The longest petiole was recorded as value "*a*," and the shorter petiole length was recorded as value "*b*." The two different species of *Boerhavia* measured were:

Boerhavia diffusa L. is a species that ranges throughout Africa, Asia, Southwestern USA, Mexico, and Central and South America. Specimens measured in this analysis were from BRIT, SHST, and TEX herbaria; consequently the range of measured specimens was mostly across the state of Texas, with various outliers from the Southeastern United States and Central and South America (Appendix 1).

Boerhavia erecta L. is native to Southwestern USA, Mexico, and Central and South America. However, it has become an adventive weed in Africa and Asia. Two to three pairs of opposite leaves, directly below the apical meristem, from 80 different individuals in a local population of *B. erecta* growing in Puerto Vallarta, Mexico (Appendix 2), were measured in June 2016. *Boerhavia erecta* is a glabrous species compared to *B. diffusa*, which is densely glandular.

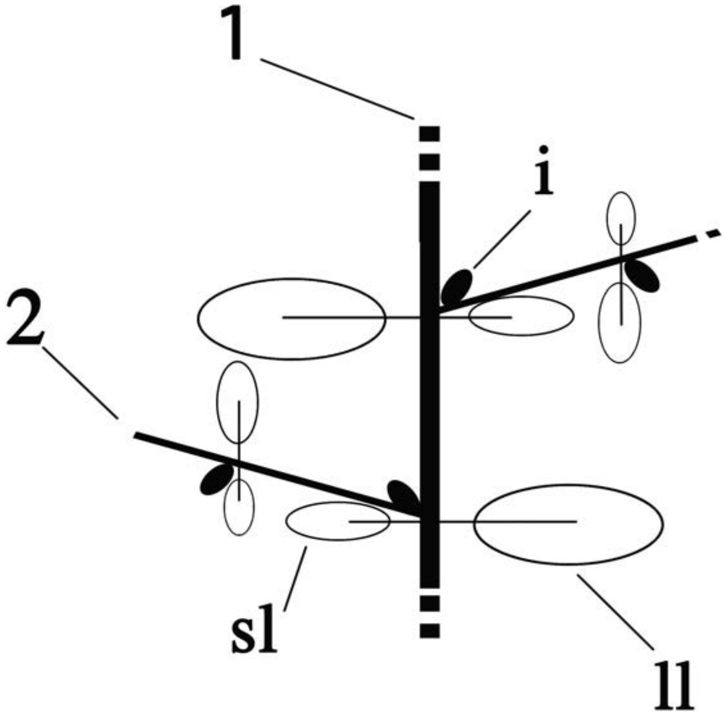


Fig. 2. Illustration of anisophylly and anisoclady in *Boerhavia*. (1) Main stem. (2) Lateral branch. (sl) small leaf. (ll) large leaf. (i) node. Illustration from Pratt and Clark (2010).

The ratio (Φ) of the opposing petiole lengths was then determined using the formula:

$$\varphi = \frac{a + b}{a} = \frac{a}{b}$$

The petiole ratios of measured leaves were then compared to the Golden Ratio using a one-paired t-test around a critical mean (Table 1). In addition, the ratios of *a/b* to *(a+b)/a* of *B. diffusa* and *B. erecta* were tested for significant deviation using a two-paired t-test (Table 2).

RESULTS

Boerhavia diffusa

A total of 258 petiole measurements were made for *B. diffusa* (Appendix 1), 129 measurements for the long petiole (*a*) and 129 for the short petiole (*b*). The range of measurements for petiole *a* was 2.4–28.83 mm, the mean value 10.689 mm, and the median value 9.62 mm. The range of measurements for petiole *b* was 1.56–17.03 mm, the mean value 6.59 mm, and the median value 5.85 mm.

The one paired t-test for a critical mean comparing the *a/b* petiole ratios of *B. diffusa* to the Golden Ratio indicates that the differences are not statistically significant. For this test the sample size (N) was 129, giving the total degrees of freedom (df) as 128. The mean value (x) for the 129 samples was 1.61872, 0.000684 from the critical value (Φ) of the Golden Ratio. The standard error of the mean (SEM) was 0.01525 with a standard deviation (SD) of 0.17325. The two-tailed P value was 0.9643, and the t value was 0.0449.

Table 1. One-paired t-test for a critical mean. Comparing actual mean to expected mean (1.6180339887…).

	B. diffusa		*B. erecta*		**Both species**	
	a/b	**(a+b)/a**	**a/b**	**(a+b)/a**	**a/b**	**(a+b)/b**
N	129	129	171	171	300	300
Df	128	128	170	170	299	299
T	0.0449	1.1326	1.8769	0.4573	1.4306	0.3132
SEM	0.01525	0.00516	0.013	0.005	0.0099	0.0037
SD	0.17325	0.05861	0.16897	0.06792	0.17094	0.06411
Mean (x)	1.61872	1.62388	1.64229	1.61566	1.63215	1.61919
two-tailed P value	0.9643	0.2595	0.0622	0.6481	0.1536	0.7543
X - Φ	0.00685	0.005845	0.02425	-0.002375	0.01412	0.001159

Table 2. Two-paired t-test comparing the *a/b* to *(a+b)/a* petiole ratios of *B. diffusa*, *B. erecta*, and both species.

	B. diffusa	*B. erecta*	**Both species**
N	129	171	300
Df	128	170	299
T	0.2537	1.4784	0.9603
SEM	0.020	0.018	0.013
X (*a/b*) - X (*a+b)/a*	-0.00516	0.026628	0.012959
two-tailed P value equals	0.8001	0.1411	0.3377

The one paired t-test for a critical mean comparing the *(a+b)/a* petiole ratios of *B. diffusa* to the Golden Ratio indicates that the differences are not statistically significant. For this test the sample size (N) was 129, giving the total degrees of freedom (df) as 128. The mean value (x) for the 129 samples was 1.62388, 0.00585 from the critical value (Φ) of the Golden Ratio. The standard error of the mean (SEM) was 0.00516 with a standard deviation (SD) of 0.05861. The two-tailed P value was 0.2595, and the t value was 1.1326.

The two paired t-test comparing the *a/b* to the *(a+b)/a* petiole ratios of *B. diffusa* indicates that the differences are not statistically significant (Table 2). For this test the sample size (N) was 129, giving the total degrees of freedom (df) as 128. The mean of *a/b* minus the mean of *(a+b)/a* equals -0.00516. The 95% confidence interval of this difference ranged from -0.045408 to 0.035088. The standard error of the mean (SEM) was 0.020. The two-tailed P value was 0.8001, and the t value was 0.2537.

Boerhavia erecta

A total of 342 petiole measurements were made for *B. erecta* (Appendix 2), 171 measurements for the long petiole (*a*) and 171 for the short petiole (*b*). The range of measurements for petiole *a* was 4.15–32.07 mm, the mean value 14.72 mm, and the median value 14.40 mm. The range of measurements for petiole *b* was 2.26–19.64 mm, the mean value 9.04 mm, and the median value 8.63 mm.

The one paired t-test for a critical mean comparing the *a/b* petiole ratios of *B. erecta* to the Golden Ratio indicates that the differences are not statistically significant. For this test the sample size (N) was 171, giving the total degrees of freedom (df) as 170. The mean value (x) for the 171 samples was 1.64229, 0.02425 from the critical value (Φ) of the Golden Ratio. The standard error of the mean (SEM) was 0.013 with a standard deviation (SD) of 0.16897. The two-tailed P value was 0.0622, and the t value was 1.8769.

The one paired t-test for a critical mean comparing the *(a+b)/a* petiole ratios of *B. erecta* to the Golden Ratio indicates that the differences are not statistically significant. For this test the sample size (N) was 171, giving the total degrees of freedom (df) as 170. The mean value (x) for the 171 samples was 1.61566, -0.002375 from the critical value (Φ) of the Golden Ratio. The standard error of the mean (SEM) was 0.005 with a standard deviation (SD) of 0.06792. The two-tailed P value was 0.6481, and the t value was 0.4573.

The two paired t-test comparing the *a/b* to the *(a+b)/a* petiole ratios of *B. erecta* indicates that the differences are not statistically significant (Table 2). For this test the sample size (N) was 171, giving the total degrees of freedom (df) as 170. The mean of *a/b* minus the mean of *(a+b)/a* equals 0.026628. The 95% confidence interval of this difference ranged from -0.008926 to 0.062182. The standard error of the mean (SEM) was 0.018. The two-tailed P value was 0.1411, and the t value was 1.4784.

Boerhavia both species
The one paired t-test for a critical mean comparing the *a/b* petiole ratios of both species of *Boerhavia* to the Golden Ratio indicates that the differences are not statistically significant. For this test the sample size (N) was 300, giving the total degrees of freedom (df) as 299. The mean value (x) for the 300 samples was 1.63215, 0.014119 from the critical value (Φ) of the Golden Ratio. The standard error of the mean (SEM) was 0.009869 with a standard deviation (SD) of 0.17094. The two-tailed P value was 0.1536 and the t value was 1.4306.

The one paired t-Test for a critical mean comparing the *(a+b)/a* petiole ratios of both species of *Boerhavia* to the Golden Ratio indicates that the differences are not statistically significant. For this test the sample size (N) was 300, giving the total degrees of freedom (df) as 299. The mean value (x) for the 300 samples was 1.61919, 0.001159 from the critical value (Φ) of the Golden Ratio. The standard error of the mean (SEM) was 0.0037 with a standard deviation (SD) of 0.06411. The two-tailed P value was 0.7543, and the t value was 0.3132.

The two paired t-test comparing the *a/b* to the *(a+b)/a* petiole ratios of both species of *Boerhavia* indicates that the differences are not statistically significant (Table 2). For this test the sample size (N) was 300, giving the total degrees of freedom (df) as 299. The mean of *a/b* minus the mean of *(a+b)/a* equals 0.012959. The 95% confidence interval of this difference ranged from -0.013599 to 0.039517. The standard error of the mean (SEM) was 0.013. The two-tailed P value was 0.3377, and the t value was 0.9603.

DISCUSSION

The results indicate that the ratios of anisophyllous petiole lengths in *Boerhavia diffusa* and *B. erecta* are similar to and not statistically different from the Golden Ratio (Tables 1, 2; Fig. 3). This data is novel because until now a phyllotactic spiral, rather than a line segment, has been the major example of phi reported in leaf development.

A literature review suggests that similar results may also be present in related anisophyllous taxa. Pratt and Clark (2010) reported length leaf ratios for several anisophyllous species of Amaranthaceae. Both the Amaranthaceae and Nyctaginaceae belong to the Order Caryophyllales suborder Caryophyllineae. The leaf length ratios reported by Pratt and Clark (2010) for the anisophyllous taxa fell between 0.54–0.69 with an average ratio of 0.59. Because the average leaf pair ratios fall very near the reciprocal value of phi (0.6180339887....) it is perhaps worth examining anisophyllous Amaranthaceae in closer detail to see if their leaves also approximate the Golden Ratio.

Another author (Heimerl 1901) presented leaf length and width measurements for the Nyctaginaceae species *Pisonia heterophylla* Choisy (Table 3). In the text Heimerl (1901) mentioned the pronounced anisophylly of *P. heterophylla*, but provided no discussion. By taking the measurements Heimerl (1901) provided and analyzing them through the formulas *(a+b)/a = a/b* we see values between the range 1.57–1.76 (Table 3) with an average of 1.645. A one-paired t-test for a critical mean demonstrates that these values are also not statistically different from the Golden Ratio. It is noted that neither Heimerl (1901) or Pratt and Clark (2010) clarified whether the reported leaf measurements included the petiole or were restricted to the leaf blade.

Given that other species of plants exhibit the tendency towards the Golden ratio in both length and area, it seems that the observations here are not unique, but rather represent a potential trend in the development of anisophyllous leaves in the Caryophyllineae.

The leading hypothesis proposed for the function of anisophylly suggests that it increases photosynthetic potential by improving light capture through the reduction of self-shading of the lower leaves (Muelbert et al. 2010). Although a valid and tested hypothesis, this explanation does not help to explain anisophylly in

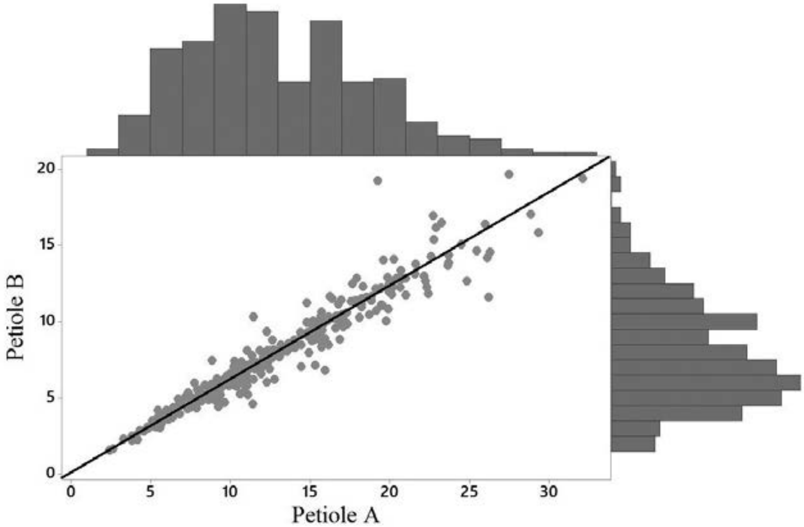


Fig. 3. Graph of the petioles from the 300 samples measured. The ideal Golden Ratio is represented by the black slope. Histograms represent the number samples at the respective measurements. X axis represents the longer petiole length; petiole *a*. Y axis represents the shorter petiole length; petiole *b*. Measurements are in millimeters.

Table 3. Three measurements of *Pisonia heterophylla* leaf length and width from Heimerl (1901), where "*a*" equals the large leaf and "*b*" the short leaf. The value for Ψ=*a/b* was calculated using the formula: $(L_a/W_a)/(L_b/W_b)$: where "L_a" = length of large leaf, "W_a" width of large leaf, "L_b" length of short leaf, "W_b" width of short leaf. The value for Ψ=(*a*+*b*)/*a* was calculated using the formula $((L_a/W_a)+(L_b/W_b))/(L_a/W_a)$. Note that the ratios of the ratios approximate the Golden Ratio.

Leaf	Measurement	*a* (large leaf)	*b* (short leaf)	Formula	Value
1	Length mm	110	50	=*a/b*	1.65
	Width mm	40	30	=(*a*+*b*)/*a*	1.61
2	Length mm	156	73	=*a/b*	1.69
	Width mm	53	42	=(*a*+*b*)/*a*	1.59
3	Length mm	160	75	=*a/b*	1.76
	Width mm	63	52	=(*a*+*b*)/*a*	1.57

Boerhavia and the Amaranthaceae as the species reported display habitual anisophylly (horizontal growth with anisophylly expressed throughout the species) rather than lateral anisophylly (upright species with anisophylly limited to plagiotrophic lateral shoots), and often grow in bright xeric habitats (Pratt & Clark 2010). Pratt and Clark (2010) demonstrated that within the Amaranthaceae anisophylly was associated with photosynthetic pathway. All of the studied species of Amaranthaceae reported with anisophylly exhibit C_4 photosynthesis while the isophyllous species demonstrated C_3 photosynthesis. Coincidently, both *B. diffusa* and *B. erecta* were recently reported to exhibit C_4 photosynthesis (Ajao et al. 2017; Note: in their paper, Ajao et al. identified *B. diffusa* as *B. coccinea*. I follow Woodson et al. (1961) and Procher (1978) in recognizing *B. coccinea* as a synonym of *B. diffusa*). To quote Pratt and Clark (2010), "any hypothesis of the adaptive significance of anisophylly and anisoclady within the (Caryophyllineae) must also take into account the correlation of these characters with photosynthetic system."

A phenomenon that typically occurs with anisophylly is anisoclady. Anisoclady is "an unequal development of the lateral shoots at the same node" (Keller 2004). *Boerhavia* is no exception in exhibiting anisoclady together with anisophylly. In the particular case of *Boerhavia*, the node that develops into a lateral stem arises from the node of the smaller leaf. The pattern of lateral branching alternates down the stem of *Boerhavia,* always developing from the node of the smaller leaf (Fig. 2). One of the immediate observations when examining lateral branching in *Boerhavia* is that apical dominance does not appear to be in effect. Lateral branching from the node of the smaller leaf directly below the apical bud occurs regularly in *Boerhavia*. It remains unclear if anisophylly and anisoclady are adaptations that override apical dominance in *Boerhavia,* or reciprocally if anisophylly and anisoclady are mere externalities of an adaptation towards the loss of apical dominance. Regardless, the question as to whether or not anisophylly has any involvement in the loss of apical dominance could provide interesting avenues of future research and hypothesis testing.

Phillips (1976) speculated for the Nyctaginaceae genus *Allionia* that anisoclady was an adaptation to its extreme environment:

> The large woody taproot, prostrate growth form with trailing stems, sympodial pattern of growth due to anisoclady, and C_4 photosynthetic physiology enable the plants to produce abundant vegetative and reproductive growth under favorable growing conditions yet to slow initiation of new growth or go completely dormant under adversity.

Similar to *Allionia, Boerhavia* demonstrates C_4 photosynthetic physiology and grows in the same xeric environment. In a reiteration of Pratt and Clark (2010), when considering the adaptive significance of anisophylly and anisoclady in the Nyctaginaceae, photosynthetic physiology should be taken into account.

There are two different processes that can account for the differences in the lengths of opposite pairs of *Boerhavia* petioles, cell proliferation or cell expansion (Hepworth & Lenhard 2014; Powell & Lenhard 2012). Currently, it is not known whether the difference in the petiole length of the anisophyllous leaves in *Boerhavia* is due to the longer petioles having more cells than the shorter petioles or whether the longer petioles have cells that are larger than the cells in the shorter petioles. A histological study (Dengler 1983) of the anisophyllous species *Selaginella martensii* indicates that anisophylly in that species is due to cell proliferation. The author further concludes that final organ size in anisophyllous taxa "more often exists between cell number … than between cell size." It is suggested here that anisophylly in *Boerhavia* is the result of cell proliferation, given that it is the mechanism most commonly reported for anisophyllous taxa and given that asymmetry in *Boerhavia* leaf size is demonstrated almost immediately when the leaves are still relatively small. A histological study comparing the size and number of cells of opposite pairs of petioles in *Boerhavia* seems the logical next step in continuing this research. However, such data collection and analysis is beyond the scope of this paper and the skill set of the author.

Regardless, the real mystery is determining the mechanism that stimulates the anisophyllous growth in *Boerhavia* to reflect the Golden Ratio. One such explanation is the reaction-diffusion model proposed by Turing (1952). Fujita et al. (2011) provide a reaction-diffusion based mathematical model for shoot apical meristem growth patterns. Unfortunately, none of the patterns they present match what is observed in *Boerhavia*. Nevertheless, the reaction-diffusion model appears to have some support, as Cooke (2006) wrote "it seems plausible that the mathematical rules for phyllotaxis arise from local inhibitory interactions among existing primordia," and although not technically phyllotaxy, the development of the asymmetric leaf pairs in *Boerhavia* is possibly the result of differential inhibition of the stem primordial.

Because the anisophyllous leaves of *Boerhavia* exhibit the Golden Ratio as a line segment it is suggested here that *Boerhavia* could be an effective model organism for furthering the studies in the genetic and physiological basis for leaf growth and development. Further studies in the asymmetric leaf growth of *Boerhavia* should focus on determining whether its leaf growth is a product of cell proliferation or cell expansion. If it is due to cell proliferation, then studies on *Boerhavia* could further determine which of the precise organ size pathways—1) cell recruitment to the primordia, 2) cell proliferation, or 3) proliferation arrest—is responsible for the asymmetric growth.

APPENDIX 1

Petiole measurements and specimens for *Boerhavia diffusa*.

Species	Herbarium	Specimen	Location	*a*	*b*	*a/b*	*(a+b)/b*
B. diffusa	BRIT	Thomas 82649	USA; LA; Cameron Co.	6.81	4.67	1.45824411	1.68575624
B. diffusa	BRIT	Thomas 67257	USA; LA; Desoto Co.	8.48	5.27	1.60910816	1.62146226
B. diffusa	BRIT	Thomas 67257	USA; LA; Desoto Co.	12.3	8.12	1.51477833	1.66016260
B. diffusa	BRIT	Thomas 66943	USA; LA; Calcasieu Co.	10.45	6.75	1.54814815	1.64593301
B. diffusa	BRIT	Thomas 66206	USA; LA; Orleans Co.	17.07	10.43	1.63662512	1.61101347
B. diffusa	BRIT	Steven Marshall 6648	Nicaragua, Dept. Managua	6.22	3.98	1.56281407	1.63987138
B. diffusa	BRIT	Spellenberg 13275	USA; AZ; Maricopa Co,	8.31	5.09	1.63261297	1.61251504
B. diffusa	BRIT	Spellenberg 13275	USA; AZ; Maricopa Co,	15.21	9.16	1.66048035	1.60223537
B. diffusa	BRIT	Spellenberg 12465	USA; FL; Palm Beach Co,	16.64	10.36	1.60617761	1.62259615
B. diffusa	BRIT	Schallert 20762	USA; FL; Fort Myers Co.	14.43	8.47	1.70365998	1.58697159
B. diffusa	BRIT	McCart 9431	USA; FL; Palm Beach Co,	15.49	9.19	1.68552775	1.59328599
B. diffusa	BRIT	Mackford 2755	Mexico; Guerrero	11.05	6.13	1.80261011	1.55475113
B. diffusa	BRIT	Leonard 3471	USA; NC; New Hanover Co.	6.37	4.09	1.55745721	1.64207221
B. diffusa	BRIT	Leonard 3471	USA; NC; New Hanover Co.	6.23	4.01	1.55361596	1.64365971
B. diffusa	BRIT	Judith Hall 7874	Nicaragua, Dept. Masaya	11.52	7.09	1.62482370	1.61545139
B. diffusa	BRIT	Hess & Massey 1432	USA; NM; Grant Co.	14.01	8.26	1.69612591	1.58957887
B. diffusa	BRIT	Dickey 176	Mexico; Nuevo Leon	8.15	4.79	1.70146138	1.58773006
B. diffusa	BRIT	Curtiss 2335	USA; FL; Hilsboro River Co.	9.15	4.9	1.86734694	1.53551913
B. diffusa	BRIT	Curtiss 2335	USA; FL; Hilsboro River Co.	6.34	4.02	1.57711443	1.63406940
B. diffusa	BRIT	Crane 540	Belize; Corozal District	28.83	17.03	1.69289489	1.59070413
B. diffusa	BRIT	Crane 540	Belize; Corozal District	22.58	14.26	1.58345021	1.63153233
B. diffusa	BRIT	Churchill s.n.	USA; FL; Orange Co.	8.56	5.2	1.64615385	1.60747664
B. diffusa	BRIT	Beaman 6270	Mexico; Veracruz	15.48	9.98	1.55110220	1.64470284
B. diffusa	BRIT	Beaman 6270	Mexico; Veracruz	13.99	8.76	1.59703196	1.62616154
B. diffusa	SHSU	SHSU	USA, TX, Walker Co.	16.11	10.07	1.59980139	1.62507759
B. diffusa	SHSU	SHSU	USA, TX, Walker Co.	16.87	10.2	1.65392157	1.60462359
B. diffusa	SHSU	SHSU	USA, TX, Walker Co.	7.5	4.77	1.57232704	1.63600000
B. diffusa	TEX	MV 14060	Guatemala; Huehuetenago	7.98	5.2	1.53461538	1.65162907
B. diffusa	TEX	MV 14060	Guatemala; Huehuetenago	11.81	8.11	1.45622688	1.68670618
B. diffusa	TEX	Huft 1912	Panama; Farfan Beach	15.66	10.33	1.51597289	1.65964240
B. diffusa	TEX	Correll 43406	West Indies: Caicos Islands	11.3	7.25	1.55862069	1.64159292
B. diffusa	TEX	Cobar 800	Guatemala; El Progreso	10.21	7.03	1.45234708	1.68854065
B. diffusa	TEX	95148	Mexico; Morelos	6.41	4.38	1.46347032	1.68330733
B. diffusa	TEX	456776	USA; TX; Matagorda Co.	8.52	5.28	1.61363636	1.61971831
B. diffusa	TEX	456714	USA; TX; Bell Co.	7.63	4.51	1.69179601	1.59108781
B. diffusa	TEX	456712	USA; TX; Travis Co.	6.82	3.95	1.72658228	1.57917889
B. diffusa	TEX	456711	USA; TX; Hays Co.	15.75	9.41	1.67375133	1.59746032
B. diffusa	TEX	434713	USA; TX; Guadalupe Co.	9.74	5.97	1.63149079	1.61293634
B. diffusa	TEX	434713	USA; TX; Guadalupe Co.	10.37	5.73	1.80977312	1.55255545
B. diffusa	TEX	434713	USA; TX; Guadalupe Co.	6.94	4.67	1.48608137	1.67291066
B. diffusa	TEX	434713	USA; TX; Guadalupe Co.	10.18	5.83	1.74614065	1.57269155
B. diffusa	TEX	299122	USA; TX; Travis Co.	10.11	6.09	1.66009852	1.60237389
B. diffusa	TEX	299122	USA; TX; Travis Co.	5.72	3.69	1.55013550	1.64510490
B. diffusa	TEX	299120	USA; TX; Travis Co.	9.75	6.24	1.56250000	1.64000000
B. diffusa	TEX	299120	USA; TX; Travis Co.	19.93	11.96	1.66638796	1.60010035
B. diffusa	TEX	299120	USA; TX; Travis Co.	10.89	6.71	1.62295082	1.61616162
B. diffusa	TEX	299120	USA; TX; Travis Co.	5.02	3.14	1.59872611	1.62549801
B. diffusa	TEX	299119	USA; TX; McLennan Co.	7.52	4.93	1.52535497	1.65558511
B. diffusa	TEX	299116	USA; TX; Cameron Co.	19.16	10.74	1.78398510	1.56054280
B. diffusa	TEX	299116	USA; TX; Cameron Co.	24.82	12.65	1.96205534	1.50966962
B. diffusa	TEX	299115	USA; TX; Cameron Co.	9.72	5.95	1.63361345	1.61213992
B. diffusa	TEX	299112	USA; TX; Cameron Co.	9.74	6.45	1.51007752	1.66221766
B. diffusa	TEX	299112	USA; TX; Cameron Co.	7.17	5.07	1.41420118	1.70711297
B. diffusa	TEX	299112	USA; TX; Cameron Co.	5.38	3.68	1.46195652	1.68401487
B. diffusa	TEX	299111	USA; TX; Cameron Co.	17.8	11.36	1.56690141	1.63820225
B. diffusa	TEX	299111	USA; TX; Cameron Co.	14.79	11.22	1.31818182	1.75862069
B. diffusa	TEX	299111	USA; TX; Cameron Co.	11.03	8.1	1.36172840	1.73436083
B. diffusa	TEX	299109	USA; TX; Cameron Co.	15.08	8.76	1.72146119	1.58090186

APPENDIX 1 *(continued)*

Species	Herbarium	Specimen	Location	*a*	*b*	*a/b*	*(a+b)/b*
B. diffusa	TEX	299109	USA; TX; Cameron Co.	8.67	5.53	1.56781193	1.63783160
B. diffusa	TEX	299109	USA; TX; Cameron Co.	14.41	7.05	2.04397163	1.48924358
B. diffusa	TEX	299108	USA; TX; Willacy Co.	26.08	14.16	1.84180791	1.54294479
B. diffusa	TEX	299108	USA; TX; Willacy Co.	22.73	15.37	1.47885491	1.67619886
B. diffusa	TEX	299108	USA; TX; Willacy Co.	17.65	12.45	1.41767068	1.70538244
B. diffusa	TEX	299108	USA; TX; Willacy Co.	20.71	12.79	1.61923378	1.61757605
B. diffusa	TEX	299107	USA; TX; Willacy Co.	11.4	4.62	2.46753247	1.40526316
B. diffusa	TEX	299107	USA; TX; Willacy Co.	5.62	3.78	1.48677249	1.67259786
B. diffusa	TEX	299107	USA; TX; Willacy Co.	9.62	4.68	2.05555556	1.48648649
B. diffusa	TEX	299106	USA; TX; Hidalgo Co.	7.25	5.16	1.40503876	1.71172414
B. diffusa	TEX	299103	USA; TX; Hidalgo Co.	19.86	12.87	1.54312354	1.64803625
B. diffusa	TEX	299103	USA; TX; Hidalgo Co.	17.89	11.35	1.57621145	1.63443264
B. diffusa	TEX	299103	USA; TX; Hidalgo Co.	11.61	7.3	1.59041096	1.62876830
B. diffusa	TEX	299103	USA; TX; Hidalgo Co.	7.89	5.5	1.43454545	1.69708492
B. diffusa	TEX	299102	USA; TX; Hidalgo Co.	15.91	6.8	2.33970588	1.42740415
B. diffusa	TEX	299102	USA; TX; Hidalgo Co.	15.29	7.14	2.14145658	1.46697188
B. diffusa	TEX	299099	USA; TX; Hidalgo Co.	12.74	6.2	2.05483871	1.48665620
B. diffusa	TEX	299095	USA; TX; Kleberg Co.	16.44	10.23	1.60703812	1.62226277
B. diffusa	TEX	299095	USA; TX; Kleberg Co.	12.88	7.97	1.61606023	1.61878882
B. diffusa	TEX	299095	USA; TX; Kleberg Co.	12.69	7.95	1.59622642	1.62647754
B. diffusa	TEX	299095	USA; TX; Kleberg Co.	23.61	13.67	1.72713972	1.57899195
B. diffusa	TEX	299091	USA; TX; Brewster Co.	5.57	3.03	1.83828383	1.54398564
B. diffusa	TEX	299090	USA; TX; Brewster Co.	7.73	5.97	1.29480737	1.77231565
B. diffusa	TEX	299084	USA; TX; Brewster Co.	3.82	2.2	1.73636364	1.57591623
B. diffusa	TEX	299084	USA; TX; Brewster Co.	6.36	4.18	1.52153110	1.65723270
B. diffusa	TEX	299083	USA; TX; Brewster Co.	19.43	12.2	1.59262295	1.62789501
B. diffusa	TEX	299083	USA; TX; Brewster Co.	15.16	10.01	1.51448551	1.66029024
B. diffusa	TEX	299082	USA; TX; Brewster Co.	10.18	6.11	1.66612111	1.60019646
B. diffusa	TEX	299082	USA; TX; Brewster Co.	5.82	3.71	1.56873315	1.63745704
B. diffusa	TEX	299078	USA; TX; Presidio Co.	5.37	3.41	1.57478006	1.63500931
B. diffusa	TEX	299078	USA; TX; Presidio Co.	6.73	4.94	1.36234818	1.73402675
B. diffusa	TEX	299078	USA; TX; Presidio Co.	3.3	2.3	1.43478261	1.69696970
B. diffusa	TEX	299073	USA; TX; Jeff Davis Co.	5.51	3.63	1.51790634	1.65880218
B. diffusa	TEX	299073	USA; TX; Jeff Davis Co.	9.15	6.26	1.46166134	1.68415301
B. diffusa	TEX	299073	USA; TX; Jeff Davis Co.	8.03	5.51	1.45735027	1.68617684
B. diffusa	TEX	299072	USA; TX; Jeff Davis Co.	6.49	4.05	1.60246914	1.62403698
B. diffusa	TEX	299070	USA; TX; Jeff Davis Co.	9.31	5.61	1.65953654	1.60257787
B. diffusa	TEX	299069	USA; TX; Jeff Davis Co.	8.57	4.91	1.74541752	1.57292882
B. diffusa	TEX	299069	USA; TX; Jeff Davis Co.	6.72	4.5	1.49333333	1.66964286
B. diffusa	TEX	299065	USA; TX; El Paso Co.	16.78	10.21	1.64348678	1.60846246
B. diffusa	TEX	299065	USA; TX; El Paso Co.	8.89	4.91	1.81059063	1.55230596
B. diffusa	TEX	282118	USA; TX; Galveston Co.	4.78	3.08	1.55194805	1.64435146
B. diffusa	TEX	282118	USA; TX; Galveston Co.	5.68	3.31	1.71601208	1.58274648
B. diffusa	TEX	282114	USA; TX; Washington Co.	6.13	3.97	1.54408060	1.64763458
B. diffusa	TEX	282113	USA; TX; Gonzales Co.	2.61	1.68	1.55357143	1.64367816
B. diffusa	TEX	282111	USA; TX; Caldwell Co.	7.31	4.27	1.71194379	1.58413133
B. diffusa	TEX	282104	USA; TX; Zapata Co.	4.61	2.86	1.61188811	1.62039046
B. diffusa	TEX	282104	USA; TX; Zapata Co.	2.4	1.56	1.53846154	1.65000000
B. diffusa	TEX	282104	USA; TX; Zapata Co.	4.06	2.43	1.67078189	1.59852217
B. diffusa	TEX	282102	USA; TX; Nueces Co.	9.76	6.15	1.58699187	1.63012295
B. diffusa	TEX	282100	USA; TX; Dimmit Co.	9.83	6.06	1.62211221	1.61648016
B. diffusa	TEX	282098	USA; TX; Willacy Co.	5.81	3.79	1.53298153	1.65232358
B. diffusa	TEX	282098	USA; TX; Willacy Co.	3.95	2.49	1.58634538	1.63037975
B. diffusa	TEX	282096	USA; TX; Kimble Co.	8.79	5.55	1.58378378	1.63139932
B. diffusa	TEX	282096	USA; TX; Kimble Co.	7.34	5.35	1.37196262	1.72888283
B. diffusa	TEX	282096	USA; TX; Kimble Co.	16.93	11.39	1.48639157	1.67277023
B. diffusa	TEX	282096	USA; TX; Kimble Co.	11.06	7.15	1.54685315	1.64647378
B. diffusa	TEX	282093	USA; TX; Jones Co.	12.08	7.13	1.69424965	1.59023179
B. diffusa	TEX	282093	USA; TX; Jones Co.	8.97	5.63	1.59325044	1.62764771

APPENDIX 1 *(continued)*

Species	Herbarium	Specimen	Location	*a*	*b*	*a/b*	*(a+b)/b*
B. diffusa	TEX	282092	USA; TX; Val Verde Co.	6.35	3.75	1.69333333	1.59055118
B. diffusa	TEX	282092	USA; TX; Val Verde Co.	4.54	2.79	1.62724014	1.61453744
B. diffusa	TEX	282090	USA; TX; Val Verde Co.	3.81	2.48	1.53629032	1.65091864
B. diffusa	TEX	282089	USA; TX; Brewster Co.	3.82	2.37	1.61181435	1.62041885
B. diffusa	TEX	282089	USA; TX; Brewster Co.	4.83	3.01	1.60465116	1.62318841
B. diffusa	TEX	282089	USA; TX; Brewster Co.	13.98	8.79	1.59044369	1.62875536
B. diffusa	TEX	282089	USA; TX; Brewster Co.	9.53	6.18	1.54207120	1.64847849
B. diffusa	TEX	282089	USA; TX; Brewster Co.	4.31	2.87	1.50174216	1.66589327
B. diffusa	TEX	282088	USA; TX; Presidio Co.	10.25	7.39	1.38700947	1.72097561
B. diffusa	TEX	282086	USA; TX; Reeves Co.	11.41	6.2	1.84032258	1.54338300
B. diffusa	TEX	282086	USA; TX; Reeves Co.	8.63	5.21	1.65642994	1.60370800
B. diffusa	TEX	252269	Mexico; Veracruz	8.4	5.85	1.43589744	1.69642857

APPENDIX 2

Petiole measurements for *Boerhavia erecta*. Individuals were measured from a local population in Puerto Vallarta, Mexico, July 2016.

Species a	b	a/b	(a+b)/b	
B. erecta	13.13	8.46	1.55200946	1.64432597
B. erecta	5.46	4.17	1.30935252	1.76373626
B. erecta	24.45	15.02	1.62782956	1.61431493
B. erecta	20.23	12.67	1.59668508	1.62629758
B. erecta	10.65	7.16	1.48743017	1.67230047
B. erecta	15.57	9.04	1.72234513	1.58060373
B. erecta	11.19	7.06	1.58498584	1.63092046
B. erecta	9.35	5.18	1.80501931	1.55401070
B. erecta	17.34	9.83	1.76398779	1.56689735
B. erecta	11.92	6.94	1.71757925	1.58221477
B. erecta	11.06	7.02	1.57549858	1.63471971
B. erecta	32.07	19.38	1.65479876	1.60430309
B. erecta	17.96	11.3	1.58938053	1.62917595
B. erecta	14.4	9.31	1.54672395	1.64652778
B. erecta	13.63	8.58	1.58857809	1.62949376
B. erecta	5.75	3.87	1.48578811	1.67304348
B. erecta	12.61	7.66	1.64621410	1.60745440
B. erecta	17.06	10.11	1.68743818	1.59261430
B. erecta	13.06	8.08	1.61633663	1.61868300
B. erecta	16.24	11.65	1.39399142	1.71736453
B. erecta	15.16	9.53	1.59076600	1.62862797
B. erecta	10.79	6.51	1.65745008	1.60333642
B. erecta	11.02	6.41	1.71918877	1.58166969
B. erecta	10.59	5.25	2.01714286	1.49575071
B. erecta	9.5	4.68	2.02991453	1.49263158
B. erecta	12.25	6.01	2.03826955	1.49061224
B. erecta	21.57	13.1	1.64656489	1.60732499
B. erecta	20.11	11.77	1.70858114	1.58528095
B. erecta	9.13	5.68	1.60739437	1.62212486
B. erecta	9.24	4.44	2.08108108	1.48051948
B. erecta	10.24	6.26	1.63578275	1.61132813
B. erecta	12.03	7.69	1.56436931	1.63923525
B. erecta	9.89	5.81	1.70223752	1.58746208
B. erecta	9.21	5.28	1.74431818	1.57328990
B. erecta	15.17	9.66	1.57039337	1.63678312
B. erecta	12.46	6.92	1.80057803	1.55537721
B. erecta	8.69	5.19	1.67437380	1.59723820
B. erecta	11.9	6.56	1.81402439	1.55126050
B. erecta	7.54	5.02	1.50199203	1.66578249
B. erecta	10.37	6.42	1.61526480	1.61909354

APPENDIX 2 *(continued)*

Species a	b	a/b	(a+b)/b	
B. erecta	9.87	6.35	1.55433071	1.64336373
B. erecta	10.51	7.13	1.47405330	1.67840152
B. erecta	5.47	3.52	1.55397727	1.64351005
B. erecta	13.6	8.28	1.64251208	1.60882353
B. erecta	10.37	7.24	1.43232044	1.69816779
B. erecta	15.24	8.81	1.72985244	1.57808399
B. erecta	19.11	12.15	1.57283951	1.63579278
B. erecta	12.61	8.78	1.43621868	1.69627280
B. erecta	15.6	9.82	1.58859470	1.62948718
B. erecta	12.69	8.13	1.56088561	1.64066194
B. erecta	21.6	13.75	1.57090909	1.63657407
B. erecta	22.72	16.94	1.34120425	1.74559859
B. erecta	18.83	11.63	1.61908856	1.61763144
B. erecta	18.71	10.46	1.78871893	1.55905933
B. erecta	15.69	10.61	1.47879359	1.67622690
B. erecta	23.69	14.34	1.65202232	1.60531870
B. erecta	25.98	16.37	1.58704948	1.63010008
B. erecta	18.54	11.59	1.59965487	1.62513484
B. erecta	16.96	10.44	1.62452107	1.61556604
B. erecta	16.15	10.31	1.56644035	1.63839009
B. erecta	18.2	11.11	1.63816382	1.61043956
B. erecta	20.99	12.84	1.63473520	1.61171987
B. erecta	13.53	8.06	1.67866005	1.59571323
B. erecta	11.54	6.88	1.67732558	1.59618718
B. erecta	23.22	16.48	1.40898058	1.70973299
B. erecta	20.67	13.34	1.54947526	1.64537978
B. erecta	18.27	11.48	1.59146341	1.62835249
B. erecta	14.83	9.28	1.59806034	1.62575860
B. erecta	16.13	8.46	1.90661939	1.52448853
B. erecta	19.75	10.03	1.96909272	1.50784810
B. erecta	20.15	12.24	1.64624183	1.60744417
B. erecta	17.57	11.33	1.55075022	1.64484917
B. erecta	6.1	3.58	1.70391061	1.58688525
B. erecta	11.12	6.92	1.60693642	1.62230216
B. erecta	8.85	7.45	1.18791946	1.84180791
B. erecta	11.35	7.77	1.46074646	1.68458150
B. erecta	17.9	12.82	1.39625585	1.71620112
B. erecta	15.62	9.96	1.56827309	1.63764405
B. erecta	20.43	12.84	1.59112150	1.62848752
B. erecta	10.88	5.42	2.00738007	1.49816176
B. erecta	18.85	11.37	1.65787159	1.60318302
B. erecta	11.44	10.31	1.10960233	1.90122378
B. erecta	4.15	2.26	1.83628319	1.54457831
B. erecta	13.81	8.33	1.65786315	1.60318610
B. erecta	9.07	4.85	1.87010309	1.53472988
B. erecta	10.2	5.89	1.73174873	1.57745098
B. erecta	19.22	19.21	1.00052056	1.99947971
B. erecta	14.82	9.08	1.63215859	1.61268556
B. erecta	5.3	3.09	1.71521036	1.58301887
B. erecta	10.64	5.98	1.77926421	1.56203008
B. erecta	8.6	4.86	1.76954733	1.56511628
B. erecta	14.93	7.95	1.87798742	1.53248493
B. erecta	8.8	5.88	1.49659864	1.66818182
B. erecta	9.96	6.57	1.51598174	1.65963855
B. erecta	7.48	4.39	1.70387244	1.58689840
B. erecta	23.66	13.85	1.70830325	1.58537616
B. erecta	13.36	8.28	1.61352657	1.61976048
B. erecta	27.47	19.64	1.39867617	1.71496178
B. erecta	29.32	15.82	1.85335019	1.53956344
B. erecta	18.31	12.28	1.49104235	1.67067176

APPENDIX 2 *(continued)*

Species a	b	a/b	(a+b)/b	
B. erecta	12.29	9.35	1.31443850	1.76078112
B. erecta	16.57	9.59	1.72784150	1.57875679
B. erecta	19.46	11.08	1.75631769	1.56937307
B. erecta	16.84	8.83	1.90713477	1.52434679
B. erecta	22.9	16.15	1.41795666	1.70524017
B. erecta	12.37	7.57	1.63408190	1.61196443
B. erecta	9.47	5.69	1.66432337	1.60084477
B. erecta	13.61	8.19	1.66178266	1.60176341
B. erecta	13.05	7.69	1.69700910	1.58927203
B. erecta	7.86	4.35	1.80689655	1.55343511
B. erecta	18.07	10.25	1.76292683	1.56723852
B. erecta	12.88	7.83	1.64495530	1.60791925
B. erecta	20.98	11.75	1.78553191	1.56005720
B. erecta	14.78	9.95	1.48542714	1.67320704
B. erecta	5.08	3.51	1.44729345	1.69094488
B. erecta	19.89	10.81	1.83996300	1.54348919
B. erecta	15.17	9.41	1.61211477	1.62030323
B. erecta	22.29	12.23	1.82256746	1.54867654
B. erecta	10.68	7.35	1.45306122	1.68820225
B. erecta	12.55	7.63	1.64482307	1.60796813
B. erecta	5.65	3.6	1.56944444	1.63716814
B. erecta	11.07	5.22	2.12068966	1.47154472
B. erecta	26.19	11.58	2.26165803	1.44215349
B. erecta	16.37	11.48	1.42595819	1.70128283
B. erecta	20.22	14.09	1.43506033	1.69683482
B. erecta	15.72	8.32	1.88942308	1.52926209
B. erecta	19.92	12.41	1.60515713	1.62299197
B. erecta	10.86	6.68	1.62574850	1.61510129
B. erecta	7.8	4.69	1.66311301	1.60128205
B. erecta	8.24	5.08	1.62204724	1.61650485
B. erecta	11.2	7.09	1.57968970	1.63303571
B. erecta	11.77	6.96	1.69109195	1.59133390
B. erecta	10.09	6.13	1.64600326	1.60753221
B. erecta	19.34	12.14	1.59308072	1.62771458
B. erecta	15.68	9.88	1.58704453	1.63010204
B. erecta	10.85	6.68	1.62425150	1.61566820
B. erecta	26.29	14.54	1.80811554	1.55306200
B. erecta	15.67	10.24	1.53027344	1.65347798
B. erecta	22.23	12.65	1.75731225	1.56905083
B. erecta	12.34	7.37	1.67435550	1.59724473
B. erecta	10.58	6.45	1.64031008	1.60964083
B. erecta	14.43	9.09	1.58745875	1.62993763
B. erecta	20.64	12.23	1.68765331	1.59253876
B. erecta	25.42	14.62	1.73871409	1.57513769
B. erecta	19.55	11.04	1.77083333	1.56470588
B. erecta	17.3	10.57	1.63670766	1.61098266
B. erecta	15.83	9.85	1.60710660	1.62223626
B. erecta	15.23	9.19	1.65723613	1.60341431
B. erecta	18.23	11.48	1.58797909	1.62973121
B. erecta	12.43	8.08	1.53836634	1.65004023
B. erecta	17.13	10.47	1.63610315	1.61120841
B. erecta	22.14	12.98	1.70570108	1.58626920
B. erecta	11.12	6.84	1.62573099	1.61510791
B. erecta	16.82	9.78	1.71983640	1.58145065
B. erecta	15.71	8.63	1.82039397	1.54933164
B. erecta	11.43	7.19	1.58970793	1.62904637
B. erecta	16.74	11.11	1.50675068	1.66367981
B. erecta	13.22	8.02	1.64837905	1.60665658
B. erecta	18.22	10.97	1.66089335	1.60208562
B. erecta	16.67	10.37	1.60752170	1.62207558

APPENDIX 2 *(continued)*

Species a	**b**	**a/b**	**(a+b)/b**	
B. erecta	19.6	14.04	1.39601140	1.71632653
B. erecta	8.95	5.71	1.56742557	1.63798883
B. erecta	9.5	6.04	1.57284768	1.63578947
B. erecta	11.92	7.36	1.61956522	1.61744966
B. erecta	8.13	4.9	1.65918367	1.60270603
B. erecta	22.41	11.84	1.89273649	1.52833556
B. erecta	12.63	7.73	1.63389392	1.61203484
B. erecta	11.03	5.82	1.89518900	1.52765186
B. erecta	5.96	4.17	1.42925659	1.69966443
B. erecta	17.05	9.66	1.76501035	1.56656891
B. erecta	15.93	8.883	1.79331307	1.55762712

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