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Comparative anatomy of invasive and non-invasive species in the family Asteraceae in Nigeria

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ABSTRACT

Comparative anatomical studies were conducted on two invasive species (*Chromolaena odorata* and *Tithonia diversifolia*) and two non-invasive species (*Ageratum conyzoides* and *Aspilia africana*) in the family Asteraceae in Nigeria. The aims are to study the anatomical characters of the invasive species and the non-invasive species with a view to report the anatomical characters in the invasive species responsible for invasiveness and also to correlate these characters with the functions they perform in the invasive species. The foliar and stem micromorphological study of the invasive and non-invasive species were undertaken using Light Microscope (LM). The occurrence of vessels in the pillar of the abundant sclerenchyma tissues are important component of the skeletal system in the invasive species. The prominent tiles of parenchymatous cells for effective conduction of water and nutrients; the occurrence of various vessel types: short and long together with wide and narrow vessels for water conservation and reduced vulnerability of stem to cavitations; the long but coiled trichomes for effective light piping; high stomata sizes with low stomatal index to reduce excessive evaporation that might lead to desiccation and severe disruption of photosynthetic function; all these among others are the characters reported for the invasive species and they are responsible for their aggressiveness and xerophytic nature.

Keywords: Micromorphology, sclerenchyma, characters, aggressive, foliar, stem.

INTRODUCTION

Biological invasions have been receiving increasing attention globally because of their significant appeal and practical connotations (Sultan, 2000; McDowell, 2002; D'Antonio et al., 2004; Burns, 2006). Invasion by non indigenous species are widely recognized as a component of human caused environmental change often resulting in significant loss in the economic value, biodiversity and function of the invaded ecosystem (Adebowale and Olorode, 2005). The invasive, non-native, alien, exotic, so called non-indigenous or introduced species

are those that evolved elsewhere and have been purposely or accidentally relocated.

The human exploration and colonization have dramatically increased the diversity and scale of invasions by introduced species that often find non natural enemies in their new habitat and therefore spread easily and quickly (Joshi, 2001). *Chromolaena odorata* is one of the highly successful and established exotic weeds. It is the highly invasive plant species in Philippines, it is hard to eradicate, a nuisance in plantations, and known to harm domesticated animals and decimate native plant species (Codilla and

Metillo, 2011). This weed is characteristic of secondary succession and it becomes a serious problem because it spreads rapidly, reduces the ecological value of bush land, reduces crop yields and reduces the carrying capacity of grazing land. It also has no value as cattle or sheep fodder and is poisonous to animals. *Chromolaena odorata* has a wide ecological range under which it can establish, grow and reproduce; the weed is reported to compete for natural resources suppressing the indigenous.

Invasive plants may have the following effects on the native floral and communities (including the processes which occur in them); decrease dominance of native species; decrease overall species richness; lower range of biodiversity over areas, changes to process such as water table levels, fire regimes, soil quality and nutrient recycling. Environmental weeds are those that invade natural vegetations which adversely affect the survival of the native floral. These invasive plants may be annual, biennial or perennial as well as perennial vines, shrubs, and trees. In general, invasive plants are characteristics of being highly adaptable to a broad range of environmental parameters. The adaptability of varying types of substrate, level of moisture, quality of light and temperature regimes allow them to invade a broad range of ecosystem and habitat types. They tend to be highly successful as adjudged, by their ability to produce abundance of seeds, and in some cases, they may have a long life in the soil seed banks (Muoghalu and Chuba, 2005).

Plant invasion poses major threat to global biodiversity conservation and are therefore regarded as a significant component of human induced environmental change (Bradley et al., 2012). *Tithonia diversifolia* and *Chromolaena odorata* are invasive plants capable of displacing other plants in their habitats (Muoghalu and Chuba, 2005). This has enabled both species to be dominant plants in most ruderal environments. A better understanding of factors determining invasibility may offer a way to predict the spatial extent, rates and directions of spread of invaders.

A lot of suggestions have been reported on ways of controlling these invasive species, some of these measures have been put into practice but even at that the invasive species kept on multiplying. Anatomical information on invasive species are very scanty, in this study, the anatomical characters of some invasive species have been studied and compared with those of the non-invasive species. In this study, the anatomical characters of *Tithonia diversifolia* and *Chromolaena odorata* (the invasive species), together with *Aspilia africana* and *Ageratum conyzoides* (the non-invasive) are compared with a view to report the anatomical characters in the invasive species responsible for invasiveness and to correlate these characters with their functions in the invasive species.

MATERIALS AND METHODS

Species of *Ageratum conyzoides*, *Aspilia africana*, *Chromolaena odorata* and *Tithonia diversifolia* were collected in Ile-Ife, Osun State and Ilorin, Kwara State, Nigeria (Table 1). The leaf and stem materials were preserved in formalin-acetic acid-alcohol (FAA). Voucher specimens were deposited in the Herbarium (IFE) of the Department of Botany, Obafemi Awolowo University, Ile-Ife, Osun State, Nigeria.

For the purpose of studying the epidermal structures, hair types and stomata, sizeable portions of the leaves were taken from the standard median portion (midway between the tip and the base) from ten specimens of each species. The portions were put in Jeffrey's maceration mixture (10% Chromic acid and bench concentrated Hydrochloric acid) and kept in the oven at 60 °C for 20 minutes. Each sample was then washed thoroughly in four to five changes of water. The abaxial and adaxial epidermes were separated by means of fine forceps and dissecting needle. The epidermes were stained in 1% safranin O for about five minutes, washed with 4 changes of water to remove excess stain and then temporary mounts were

made in 25% glycerol. Stomatal index was calculated according to Dilcher (1974).

Small blocks of stem samples were boiled in water for about two hours to soften them. Transverse sections, tangential longitudinal sections, and radial longitudinal sections were made on Reichert Sledge Microtome at varying thickness between 8- 15 μm . The sections were stained in 1% solution of Safranin O for 15 minutes, washed in three changes of water, counter-stained in 1% solution Alcian blue for 3-5 minutes, washed thoroughly in water, dehydrated through series of ethyl alcohol; 30, 50, 70, 90 and 95% with two changes in 95% alcohol in Xylene and mounted in DPX mountant.

For the purpose of maceration, small pieces of the stem of each species were macerated in Schutz's fluid, a mixture of equal of 10% solution of Chromium trioxide and 10% solution of concentrated nitric acid (Bradbury, 1973). The wood elements separate readily when teased apart with needles which were stained in 1% Safranin O and mounted on a slide using dilute glycerol as mountant. The dimension and anatomical characteristics of the vessel element and fibre were described respectively. For each sample, the length and diameter of twenty (20) vessel elements and fibres were measured from the macerated materials and expressed as a range of values (Olatunji, 1992; Metcalfe and Chalk, 1950). The fibre-length and vessel-length ratio (f/v ratio) were also calculated from the average of the fibre and vessel length obtained from each specimen.

All processed materials were preserved in 50% ethyl alcohol until when required. Illustrations were made with camera lucida fitted to M20 Wild microscope. Photomicrographs of the wood sections were taken using Leitz camera mounted on Dialux Research Microscope. All measurements were made with the aid of ocular micrometer and final figure obtained with ocular constant.

Data generated were subjected to multivariate statistical analysis method. One way analysis of variance was used to show significant difference while mean were

compared at $p < 0.05$ using Duncan Multiple Range Test from System Analysis Software.

RESULTS

Adaxial surface of *Ageratum conyzoides*

Linn.: epidermal cells are irregular, varying in size and arrangement (Figure 1a). The size ranges between 98.50 - 162.30 μm in length and 36.30 - 53.40 μm in width (Table 2). The anticlinal wall is sinuous. Venation pattern is actinodromous, marginal to basal. Stomata anomocytic, elliptical to circular in shape (Figure 1a). Stomatal size ranges between 622.10 - 1288.50 μm^2 and the stomatal index ranges between 8.40 - 16.00%. Trichomes are non- glandular, largely multicellular with simple foot (Figure 1b). Trichome length ranges between 279.30 μm - 470.00 μm with mean length of 370.00 μm .

Abaxial surface of *Ageratum conyzoides*

Linn: epidermal cells are irregular, varying in size and arrangement. The size ranges between 70.50 μm - 157.30 μm in length and between 28.30 - 37.50 μm^2 in width (Figure 1c). The anticlinal wall is sinuous. Venation pattern is actinodromous, marginal to basal. Stomata anomocytic, elliptical to circular in shape (Figure 1c), stomatal size ranges between 303.60 - 806.50 μm^2 and the stomatal index ranges between 28.50 - 40.60% (Table 2). Trichomes are non- glandular, largely multicellular with simple foot (Figures 1d and 1e). Trichome length ranges between 117.00 μm - 441.00 μm with mean length of 320.14 μm .

Stem anatomy of *Ageratum conyzoides*

Linn: wood is diffusing porous (Figure 1f). Vessels are predominantly solitary (95.85 - 85.70%), pore chain are rare (4.16 - 14.85%). Vessel shape is elliptical to circular in cross section (Figure 1f). Vessel frequency range is 33.00 - 96.00 per mm^2 , mean vessel number of 56.70 per mm^2 , vessel member diameter range is 14.40 - 25.20 μm (Figures 1f and 1j), vessel member length range 176.40 - 499.80 μm (Tables 3 and 10). Scalariform pitting and

simple pitted perforation are present (Figures 1g and 1h). Tracheid fibers are abundant, they are thin walled, with large lumen (Figure 1i) non-septate, fiber length range 411.60 - 837.00 μm . F/V ratio = 2.22. Rays are homocellular, made up of procumbent cells. The wood shows both biseriate and multiseriate rays (Figure 1g). Apotracheal parenchyma is abundant (Figure 1f).

Adaxial surface of *Aspilia Africana* (Pers)

C.D Adams: epidermal cells are irregular and occasionally polygonal, varying in size and arrangement. Epidermal cell sizes ranges between 42.41 - 36.70 μm in length and between 23.41 - 36.70 μm in width. The anticlinal wall pattern is wavy. Venation pattern is actinodromous, basal to suprabasal. Stomata are anomocytic, elliptic to circular in shape (Figure 2d). The stomatal size ranges between 324.50 - 842.00 μm^2 and the stomatal index is between 8.60 - 14.00% (Table 4). Trichomes are non-glandular, largely bicellular, apex pointed, conical, and curved, with simple foot (Figures 2e and 2f). Trichome length ranges between 132.31 μm - 661.00 μm with mean length of 347.00 μm .

Abaxial surface of *Aspilia africana* (Pers)

C.D Adams: epidermal cells are irregular, varying in size and arrangement. Epidermal cell sizes ranges between 39.72 - 56.50 μm in length and between 17.51 - 33.53 μm in width. The anticlinal wall pattern is sinous. Venation pattern is actinodromous, basal to suprabasal. Stomata are anomocytic, the shape is elliptic (Figure 2a). The stomatal size ranges between 305.20 - 720.63 μm^2 and the stomatal index is between 17.60 - 26.80% (Table 4). Trichomes are non-glandular, largely bicellular, apex pointed, conical, and curved, with 406.14 μm .

Stem anatomy of *Aspilia africana* (Pers)

C.D Adams: wood diffuse is porous (Figure 2g). The vessels are elliptical to

circular in shape with irregular arrangement (Figure 2g). Vessel frequency ranges between 7.00 - 25.00 per mm^2 , mean vessel number of 15.10 per mm^2 , vessel member diameter is between 43.20 - 93.60 μm , vessel member length ranges between 201.60 - 432.00 μm (Table 5 and 10). F/V ratio is 0.47. The fibers are very short with large lumen and thin cell wall, libriform fibers are abundant, fibre length ranges between 126.60 - 198.00 μm (Figure 2j). Rays are heterocellular, made up of procumbent and upright ray cells (Figures 2h and 2i), uniseriate, biseriate and multiseriate cells are present (Figures 2h and 2i). Tannins and resins are present. Apotracheal parenchyma abundant (Figure 2g).

Adaxial surface of *Chromolaena odorata*

Linn: epidermal cells are polygonal to irregular in shape, varying in size and arrangement. The epidermal cell sizes ranges between 67.70 - 86.42 μm in length and between 23.60 - 39.50 μm in width (Table 6). The anticlinal wall pattern is wavy. Venation pattern is actinodromous, suprabasal. Leaf surface is amphistomatic, stomata are largely anomocytic, elliptical to circular in shape (Figure 3a). Stomatal size ranges between 724.21 - 1082.30 μm^2 and the stomatal index ranges between 3.40 - 8.00%. Trichomes non-glandular trichomes, multicellular, uniseriate, coiled towards the pointed apex, simple foot; amoeboid shaped trichome was also observed (Figure 3b). Trichome length is 205.22 - 808.51 μm with mean length of 536.60 μm .

Abaxial surface of *Chromolaena odorata*

Linn: epidermal cells are irregular varying in sizes and arrangement. Epidermal cell size ranges between 59.00 - 92.90 μm in length and 17.00 - 40.72 μm in width. The anticlinal wall is deeply sinous. Venation pattern is actinodromous suprabasal. The leaf surface is amphistomatic, stomata is anomocytic, elliptical to circular in shape (Figure 3c). Stomatal sizes ranges between

430.60 - 720.52 μm^2 , and stomatal index ranges between 16.23 - 24.13% (Table 6). Trichomes non-glandular, multicellular, uniseriate, coiled towards the pointed apex, simple foot, and amoeboid shaped trichome was also observed (Figure 3d). Trichome length ranges between 176.00 - 735.00 μm with mean length of 390 μm .

Stem anatomy of *Chromolaena odorata*

Linn: wood is diffusing porous (Figure 3e). Solitary vessels ranges between 62.50 - 90.00%, pore chains are 10.00 - 37.50%. Vessels are circular to oval in shape with regular arrangement, irregular rarely occur, heavily sclerified, vessel member frequency ranges between 5.00 - 18.00 per mm^2 , mean vessel number is 9.50 per mm^2 , vessel member diameter ranges between 39.60 - 82.80 μm (Figure 3g), vessel member length ranges between 216.00 - 648.00 μm (Table 7 and 10). The fiber has large lumen and thin wall, tracheid fibers abundant, non septate fiber (Figure 3g). Fiber length ranges between 115.20 - 205.00 μm (Figure 2e). F/V ratio 0.50. Medullary rays are present, they may be uniseriate, biseriate or multiseriate (Figure 3f). Apotracheal parenchyma is abundant (Figure 3e).

Adaxial surface of *Tithonia diversifolia* (Hemsl)

A. Gray: epidermal cells are polygonal, varying in size and arrangement. Epidermal cells ranges between 54.92 - 67.50 μm in length and 19.60 - 34.80 μm in width. The anticlinal wall is deeply sinous. The venation pattern is actinodromous. Leaf surface largely amphistomatic, stomata anomocytic, and elliptical to circular in shape (Figure 4c). The stomatal size ranges between 652.61 - 960.80 μm^2 and stomatal index ranges between 8.50 - 11.00% (Table 8).

Trichomes are non-glandular, bicellular to multicellular, apex pointed, spine-like, bent towards the foot, simple foot (Figure 4d).

Trichome length is 147.01 - 250.22 μm with mean length of 273.32 μm .

Abaxial surfaces of *Tithonia diversifolia* (Hemsl)

A. Gray: epidermal cells are polygonal, varying in size and arrangement. Epidermal cell sizes ranges between 43.31 μm - 76.01 μm in length and 20.70 μm - 34.50 μm in width. The anticlinal wall is deeply sinous. The venation pattern is actinodromous. Leaf surface is amphistomatic, stomata anomocytic and elliptical to circular in shape (Figure 4a), the stomatal sizes ranges between 490.20 - 760.50 μm^2 and stomatal index ranges between 8.00 - 22.40% (Table 8). Trichome non-glandular, bicellular to multicellular, apex pointed, bent towards the base, simple foot (Figure 4b). Trichome length ranges from 132.11 - 250.31 μm with mean length of 216.42 μm .

Stem anatomy of *Tithonia diversifolia* (Hemsl)

A. Gray: wood is diffuse porous. Vessels are heavily sclerified (Figure 4e). Solitary vessels are 85.00 - 89.00%, pore chains range between 10.00 - 16.00%, they are round to oval in shape (Figure 4e). Vessel member frequency ranges between 8.00 - 15.00 per mm^2 , vessel mean number is 11.30 per mm^2 and vessel member diameter ranges between 50.40 - 82.80 μm , vessel member length ranges between 90.00 - 288.00 μm (Figure 4h). The fiber has large lumen, thin cell wall; the fibers are largely tracheid fiber, fiber length range between 360.00 - 648.00 μm (Tables 9 and 10). F/V ratio is 2.95. Medullary rays are present, rays are storied, tannins present in the rays (Figure 4e). Paratracheal parenchyma cells are abundant (Figure 4e). The wood characters of non-invasive and invasive species of the family Asteraceae studied are as summarized in Table 11.

Table 1: A list of collected data for the species of Asteraceae investigated.

Species	Author's Collection Number	Location	Collector
<i>Ageratum conyzoides</i>	FSAA1	Behind Botany Dept, O.A.U, Ile-ife, Osun State.	Awosode Orabanjo
<i>Ageratum conyzoides</i>	FSAA2	Maternity center,modakeke-ife	Adebola Temilade
<i>Ageratum conyzoides</i>	FSAA3	Kwara state college of health technology offa Kwara state	Awosika Olakanmi
<i>Ageratum conyzoides</i>	FSAA4	Ajebandele Estate, Ife-ibadan Exp. Ile-ife, Osun State.	Awosode Orabanjo
<i>Ageratum conyzoides</i>	FSAA5	Aza dam area Ilorin	Ologundudu Akinbode
<i>Ageratum conyzoides</i>	FSAA6	Onikoko Village Ondo Road ile ife.	Awosika Olakanmi
<i>Ageratum conyzoides</i>	FSAA7	Eyenkorin Area,Kwara state.	Ologundudu Akinbode
<i>Aspilia Africana</i>	FSAAS1	Maternity center Modakeke-ife	Awosode Orabanjo
<i>Aspilia Africana</i>	FSAAS2	Kwara state college of Health Technology, offa Kwara state.	Awosode Orabanjo
<i>Aspilia Africana</i>	FSAAS3	Eyenkorin Area Kwara state.	Akinbode Ologundudu
<i>Aspilia Africana</i>	FSAAS4	Famia road,Omi igbin, Modakeke, Osun State.	Orayinka Stephen
<i>Aspilia Africana</i>	FSAAS5	Aroko Quarters Ile ife	Awosode Orabanjo
<i>Aspilia Africana</i>	FSAAS6	Behind Botany Dept O.A.U, Ile-ife Osun state.	Awosode Orabanjo
<i>Chromolaena odorata</i>	FSAC1	Maternity center modakeke ife	Awosode Orabanjo
<i>Chromolaena odorata</i>	FSAC2	Famia road ile-ife	Orayinka Stephen
<i>Chromolaena odorata</i>	FSAC3	Onikoko village ile ife	Awosode Orabanjo
<i>Chromolaena odorata</i>	FSAC4	Obafemi Awolowo University Research Farm O.A.U Ile ife.	Olorungbeja John
<i>Chromolaena odorata</i>	FSAC5	Alaba meta village modakeke ife	Awosode Orabanjo

<i>Chromolaena odorata</i>	FSAC6	Aza Dam Ilorin	Adebola Orabanjo
<i>Chromolaena odorata</i>	FSAC7	Zobi road Ilorin	Afolayan Adebayo
<i>Chromolaena odorata</i>	FSAC8	Aroko Quarters ile ife	Ekperemechi Stephen
<i>Tithonia diversifolia</i>	FSAT1	Maternity center modakeke ife	Awosode Orabanjo
<i>Tithonia diversifolia</i>	FSAT2	Aroko Quartes ile ife	Awosika Olakanmi
<i>Tithonia diversifolia</i>	FSAT3	Aza dam Ilorin	Akinbode Ologundudu
<i>Tithonia diversifolia</i>	FSAT4	Kwara state College of Health Tech., Offa, Kwara State.	Oladipupo Bukola
<i>Tithonia diversifolia</i>	FSAT6	Zobi Road Ilorin	Awosode Orabanjo
<i>Tithonia diversifolia</i>	FSAT7	Alaba meta village ile ife	Adebola Temilade
<i>Tithonia diversifolia</i>	FSAT8	Okin Biscuit factory Road offa Kwara state.	Akinbode Ologundudu
<i>Tithonia diversifolia</i>	FSAT9	Ife city line 4, off Ilesha road ile ife.	Awosika Olakanmi
<i>Tithonia diversifolia</i>	FSAT10	Opa Ilesha Road ile ife	Orayinka Boye
<i>Tithonia diversifolia</i>	FSAT11	Omi igbin Area modakeke ife	Awosode Orabanjo

Table 2: Simple descriptive statistics of leaf epidermal characters of *Ageratum conyzoides*.

Variables	Minimum		Maximum		Mean		Standard Deviation		Standard error	
	Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial
X1	622.10	303.60	1288.50	806.50	864.88	607.73	207.63	200.04	65.65	63.26
X2	98.50	70.50	162.30	157.30	126.92	101.70	23.69	8.88	7.49	2.81
X3	36.30	28.30	53.40	37.50	43.54	32.95	31.21	7.12	9.84	2.25
X4	279.30	117.00	470.00	441.00	370.00	320.14	92.43	110.45	34.93	29.23

X1 = Stomatal Size (μm^2), X2 = Length of Epidermal Cell (μm), X3 = Width of Epidermal Cell (μm), X4 = Trichome Length (μm).

Table 3: Simple descriptive statistics of wood characters of *Ageratum conyzoides*.

Variables	Minimum		Mean	Standard Deviation	Standard error
	Maximum				
X1	14.40	25.20	20.64	3.12	0.99
X2	176.40	499.80	284.65	93.25	29.49
X3	33.00	96.00	56.70	21.15	6.69
X4	115.20	205.00	171.00	26.36	8.34

X1 = Vessel member diameter (μm), X2 = Vessel member length (μm), X3 = Average vessel number (μm), X4 = Fibre length (μm).

Table 4: Simple descriptive statistics of leaf epidermal characters of *Aspilia africana*.

Variables	Minimum		Maximum		Mean		Standard Deviation		Standard error	
	Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial
X1	324.50	305.20	842.00	720.63	596.41	528.93	215.29	174.00	68.08	55.03
X2	42.41	39.72	96.40	56.50	68.34	45.17	19.66	5.61	6.22	1.77
X3	23.41	17.51	36.70	33.53	27.14	40.93	5.07	11.50	1.60	3.64
X4	132.31	176.20	661.00	720.00	347.00	406.14	177.49	165.20	56.13	52.24

X1 = Stomatal size (μm^2), X2 = Epidermal cell length (μm), X3 = Epidermal cell width (μm), X4 = Trichome length (μm).

Table 5: Simple descriptive statistics of wood characters of *Aspilia africana*.

Variables	Minimum		Mean	Standard Deviation	Standard error
	Maximum				
X1	43.12	93.60	65.52	14.97	4.73
X2	201.60	432.00	333.00	88.17	27.88
X3	7.00	25.00	15.10	6.69	1.96
X4	126.60	198.00	155.88	23.64	7.48

X1 = Vessel member diameter (μm), X2 = Vessel member length (μm), X3 = Average vessel number (μm), X4 = Fibre length (μm).

Table 6: Simple descriptive statistics of leaf epidermal characters of *Chromolaena odorata*.

Variables	Minimum		Maximum		Mean		Standard deviation		Standard error	
	Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial
X1	724.21	430.60	1082.30	720.52	906.51	590.07	128.05	122.26	40.49	38.66
X2	67.70	59.00	86.42	92.90	69.72	73.53	3.53	11.19	1.12	3.54
X3	23.60	17.00	39.50	40.72	32.21	29.33	5.77	8.69	1.82	2.75
X4	205.22	176.00	808.51	735.00	536.60	390.00	188.09	155.90	57.26	49.30

X1 = Stomatal size (μm^2), X2 = Epidermal cell length (μm), X3 = Epidermal cell width (μm), X4 = Trichome length (μm)

Table 7: Simple descriptive statistics of wood characters of *Chromolaena odorata*.

Variables	Minimum	Maximum	Mean	Standard Deviation	Standard error
X1	39.60	82.80	54.00	13.47	4.26
X2	216.00	648.00	342.00	76.48	24.19
X3	5.00	18.00	9.50	4.03	1.28
X4	115.20	205.00	171.00	26.36	8.34

X1 = Vessel member diameter (μm), X2 = Vessel member length (μm), X3 = Average vessel number (μm), X4 = Fibre length (μm).

Table 8: Simple descriptive leaf epidermal characters of *Tithonia diversifolia*.

Variables	Minimum		Maximum		Mean		Standard deviation		Standard error	
	Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial
X1	652.61	490.20	960.80	760.50	855.14	669.35	122.80	81.10	38.83	25.65
X2	54.92	43.31	67.50	76.01	78.40	83.40	14.45	27.01	4.57	8.54
X3	19.60	20.70	34.80	34.50	25.42	28.38	5.93	5.47	1.87	1.73
X4	147.01	132.11	250.22	250.31	273.32	216.42	30.22	41.60	9.56	9.56

X1 = Stomatal size (μm^2), X2 = Epidermal cell length (μm), X3 = Epidermal cell width (μm), X4 = Trichome length (μm).

Table 9: Simple descriptive statistics of wood characters of *Tithonia diversifolia*.

Variables	Minimum	Maximum	Mean	Standard Deviation	Standard error
X1	50.40	82.80	63.38	12.02	3.80
X2	90.00	288.00	168.48	69.55	22.00
X3	8.00	15.00	11.30	2.06	0.65
X4	360.00	648.00	497.52	101.71	32.16

X1 = Vessel member diameter (μm), X2 = Vessel member length (μm), X3 = Average vessel number (μm), X4 = Fibre length (μm).

Table 10: Quantitative wood parameters in the four species of Asteraceae.

Character	<i>Ageratum conyzoides</i>	<i>Aspilia africana</i>	<i>Chromolaena odorata</i>	<i>Tithonia diversifolia</i>
Vessel pore diameter	20.64 ^c	65.52 ^a	54.00 ^b	63.38 ^{ab}
Vessel member length	284.65 ^a	333.00 ^a	342.00 ^a	168.48 ^b
Average vessel number	56.70 ^a	15.10 ^b	9.50 ^b	11.30 ^b
Fibre length	665.91 ^a	155.88 ^c	171.00 ^c	497.52 ^b

Mean with the same letter along a column are not significantly different ($p > 0.05$).

Table 11: Wood characters of non-invasive and invasive species in the family Asteraceae.

Characters	<i>Ageratum conyzoides</i>	<i>Aspilia Africana</i>	<i>Chromolaena odorata</i>	<i>Tithonia diversifolia</i>
Fibre/Vessel Ratio	2.22	0.47	0.50	2.95
Vessel frequency range	33.00-96.00	7.00-25.00	5.00-18.00	8.00-15.00
Vessel most frequent range	46.00-56.00	16.00-18.00	6.00-13.00	10.00-12.00
Mean vessel frequency	56.70	15.10	9.50	11.30
Vessel diameter range	14.40-25.20	43.20-93.60	39.60-82.80	50.40-82.80
Mean vessel diameter μm	20.64	65.52	54.00	63.38
Vessel length range	176.40- 499.80	201.60-432.00	216.00-648.00	90.00-288.00
Mean vessel length μm	284.65	333.00	342.00	168.48
Fibre length range	411.60-837.00	126.60-198.00	115.20-205.00	360.00-648.00
Mean fibre length μm	665.91	155.88	171.00	497.52

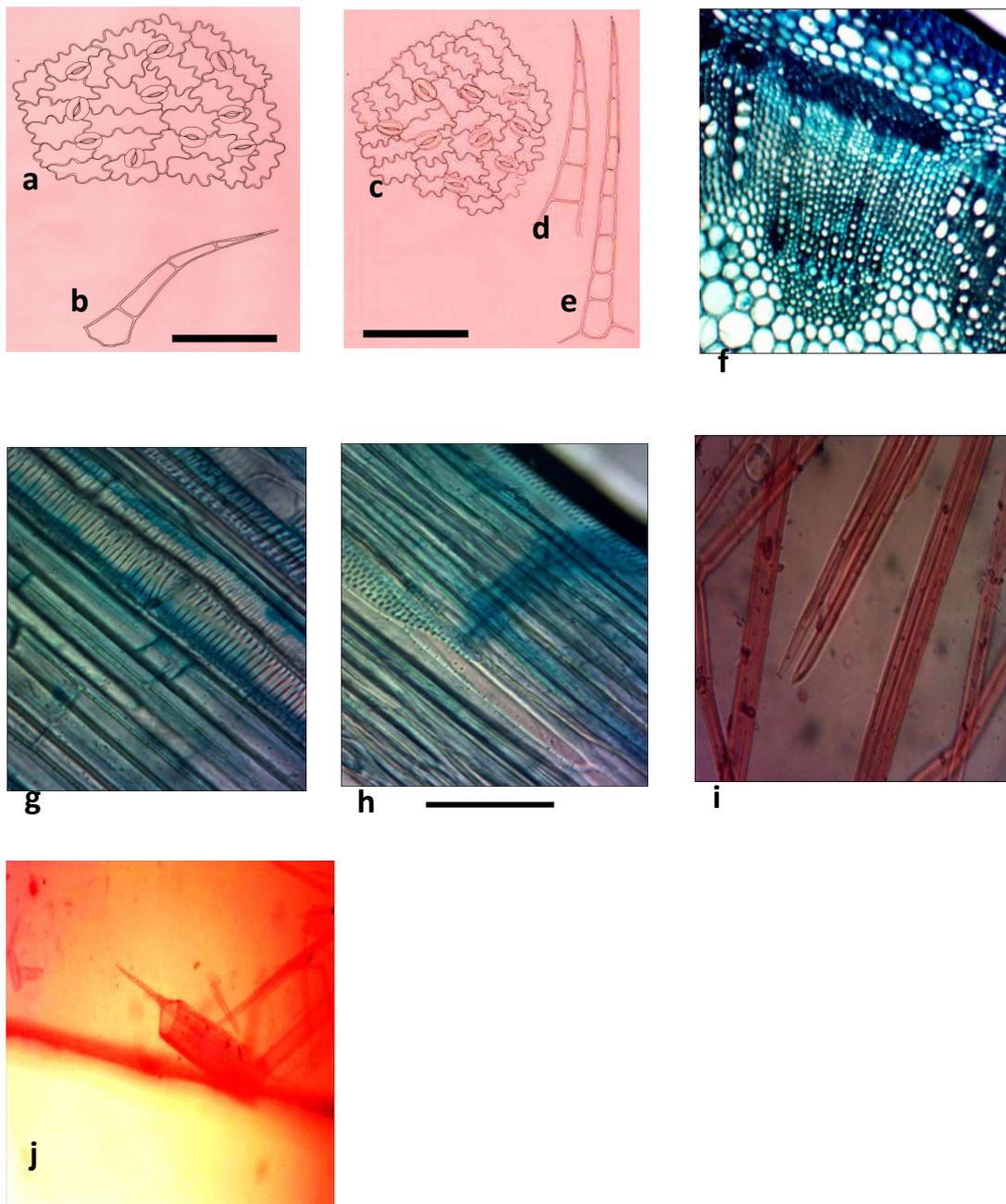


Figure 1: (a) Adaxial epidermal surface of lamina of *Ageratum conyzoides*. (b) Adaxial uniseriate, multicellular non-glandular trichome. (c) Abaxial epidermal surface of lamina of *Ageratum conyzoides* surface. (d and e) Abaxial uniseriate, multicellular non-glandular trichomes. Scale bar for figures a – e = 48 μ m. (f) Transverse section of Stem of *Ageratum conyzoides*. (g) Tangential Longitudinal Section (TLS) of Stem of *Ageratum conyzoides* with Scalariform pits. (h) Tangential Longitudinal Section (TLS) of Stem of *Ageratum conyzoides* showing vessel member. (i) Tracheid Fibre. (j) Vessel Member. Scale bars for Figures f - j = 78 μ m.

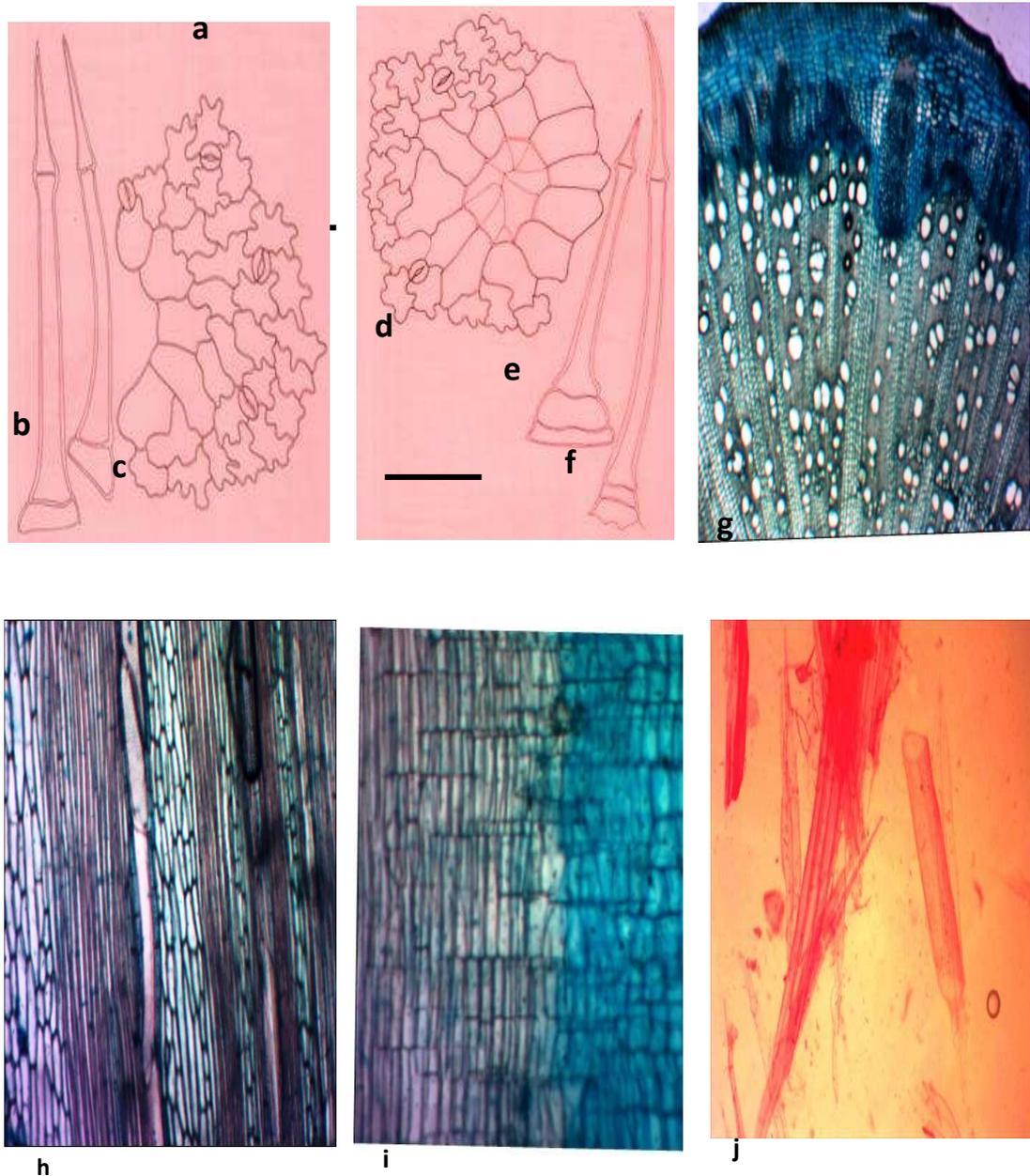


Figure 2: (a) Abaxial epidermal surface of lamina of *Aspilia africana*. (b and c) Abaxial uniseriate, multicellular non-glandular trichome. (d) Adaxial epidermal surface of lamina of *Aspilia africana*. (e and f) Adaxial uniseriate, multicellular non-glandular trichome. Scale bar for figures a – f = 48 μ m. (g) Transverse section of Stem of *Aspilia africana*. (h) Tangential Longitudinal Section (TLS) of Stem of *Aspilia africana*. (i) Radial Longitudinal Section (RLS) of Stem of *Aspilia Africana*. (j) Tracheid Fibres and Vessel. Scale bars for Figures g - j = 78 μ m.

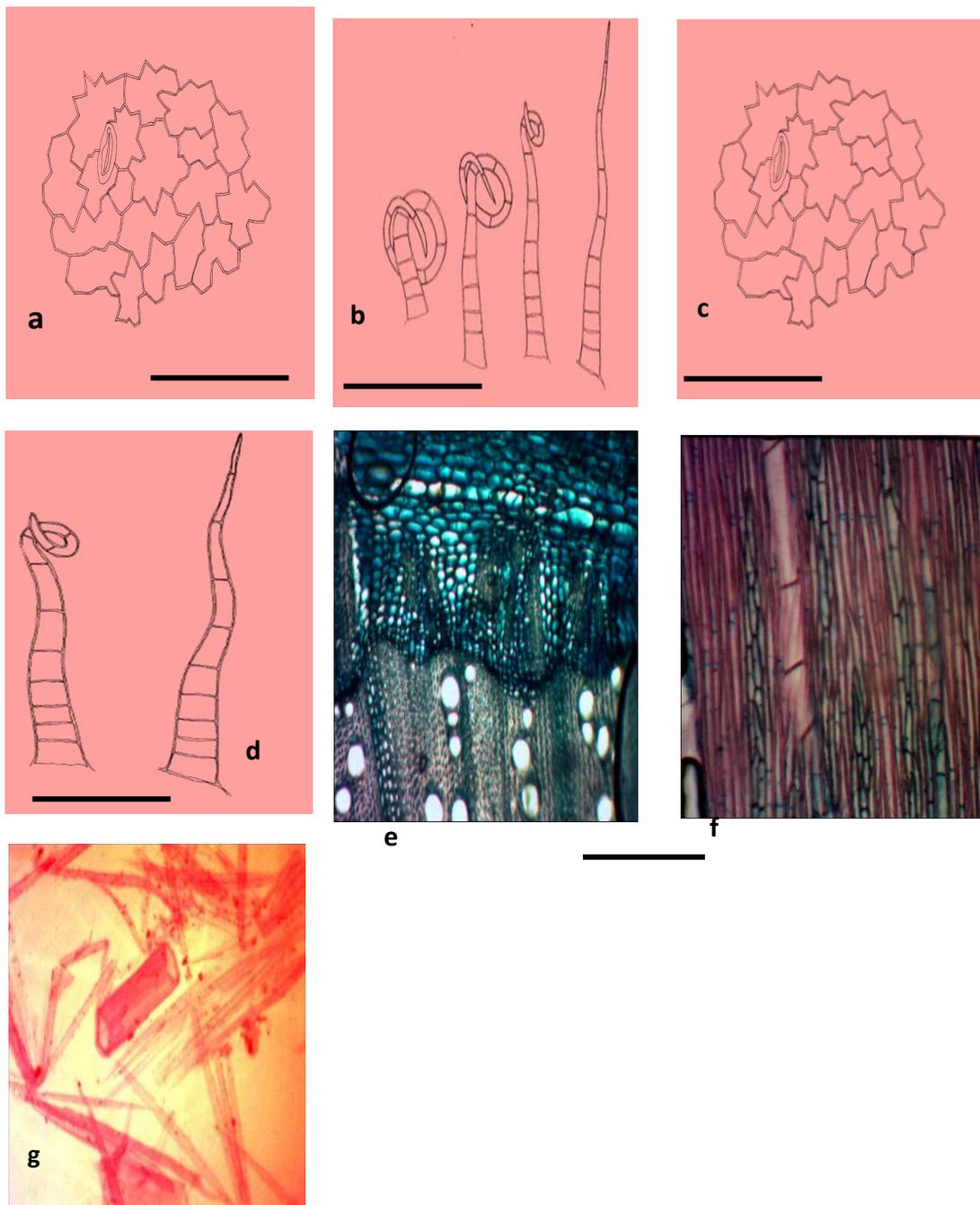


Figure 3: (a) Adaxial epidermal surface of lamina of *Chromolaena odorata*. (b) Adaxial, coiled uniseriate, multicellular non-glandular trichome. (c) Abaxial epidermal surface of lamina of *Chromolaena odorata*. (d) Abaxial, coiled uniseriate, multicellular non-glandular trichome. Scale bar for figures a – d = 48 μm. (e) Transverse section of Stem of *Chromolaena odorata*. (f) Tangential Longitudinal Section (TLS) of Stem of *Chromolaena odorata*. (g) Tracheid Fibres and Vessel. Scale bars for Figures e - g = 78 μm.

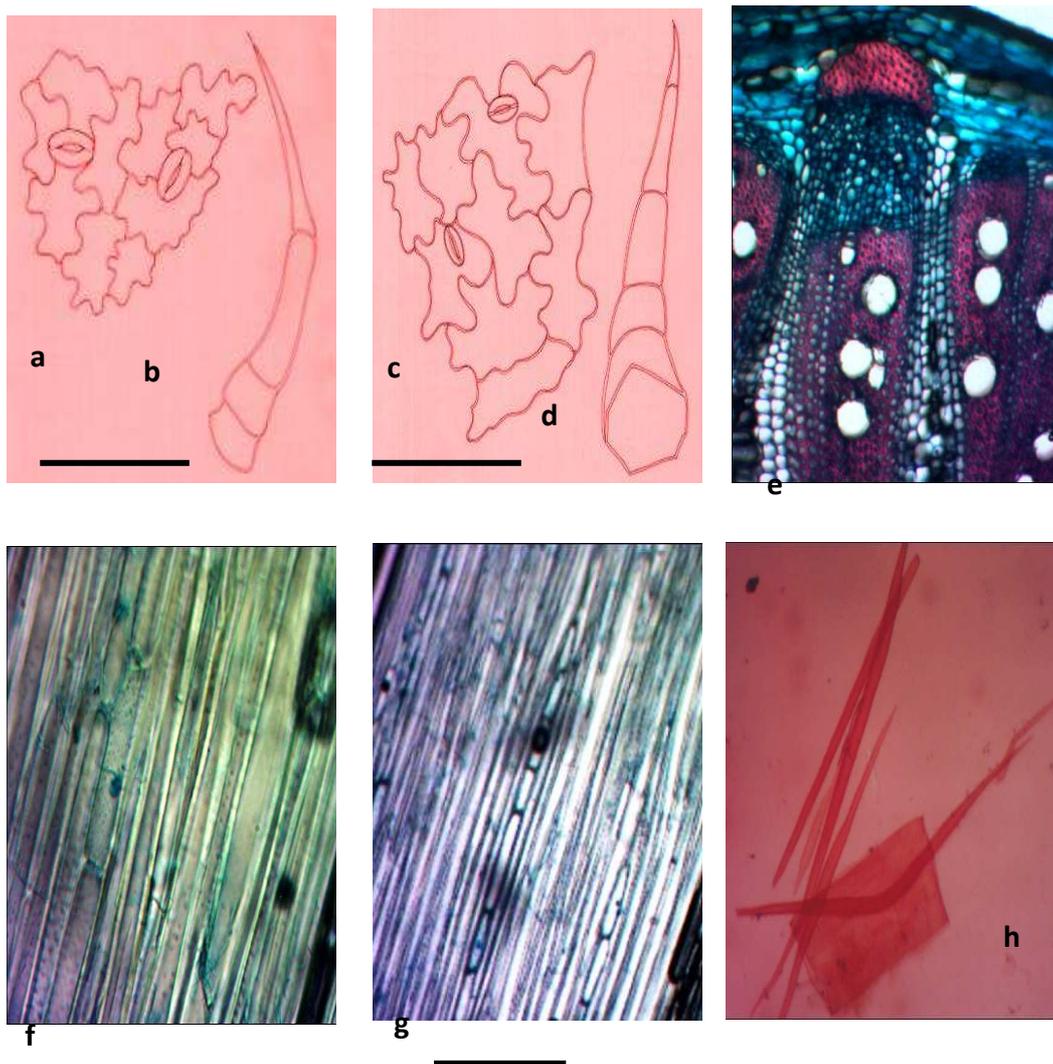


Figure 4: (a) Abaxial epidermal surface of lamina of *Tithonia diversifolia*. (b) Abaxial uniseriate, multicellular non-glandular trichome. (c) Adaxial epidermal surface of lamina of *Tithonia diversifolia*. (d) Adaxial uniseriate, multicellular non-glandular trichome. Scale bar for figures a – d = 48 μm . (e) Transverse section of Stem of *Tithonia diversifolia*. (f) Radial Longitudinal Section (RLS) of Stem of *Tithonia diversifolia*. (g) Tangential Longitudinal Section (TLS) of Stem of *Tithonia diversifolia*. (h) Tracheid Fibres and Vessel. Scale bars for Figures e -h = 78 μm .

DISCUSSION

The characters responsible for invasiveness are reported in this study, understanding these traits may improve the ability to predict, prevent, and manage invasion (Burns, 2006). Interestingly, these characters are abundant in both *Tithonia*

diversifolia and *Chromolaena odorata* which are the invasive species in this study but traces of some of these characters are noted in *Aspilia africana* (a non-invasive species), implying that in the nearest future, it may be manifesting these invasive traits. Notable among these characters is the presence of

sclerenchymatous tissues in the stem of both *Tithonia diversifolia* and *Chromolaena odorata*. These tissues form caps around the vascular tissues and the vessels are in the pillar of Sclerenchyma cells. This has greatly contributed to the resilience of the invasive species against cavitation, embolism and implosion. Hacke et al. (2001) reported that, the surrounding tissues may act to strengthen vessel walls, somehow increasing resistance to cavitation without a necessary change in the vessel thickness or lumen diameter. Sclerenchymatous tissue is an important component of the skeletal system of the plant and its abundance may be an indication of xerophytism. The development of sclerenchymatous tissues around the vessels prevents undue wilting in leaves. Sclerenchymatous tissues are adapted to withstand both compressive and tensile stresses in plants (Jarvis, 2012); they also give support to the conductive tissues for effective conduction of water and nutrients.

In the invasive species, the parenchyma cells are closely packed with prominent tiles of parenchymatous cells for effective conduction of water and nutrients whereas in *Ageratum conyzoides* and *Aspilia africana* (non-invasive species), they are loosely packed. This suggests more parenchyma cells in the invasive species than in the non-invasive species. Parenchyma cells play an important role in the repair of damage, since they are able to continuously divide throughout the life of the plant, they are able to replace and repair cells that become broken or damaged, and this allows the plant to heal itself in most cases against injury (Hacke et al., 2001). In natural ecosystems, the dominant factors relating to survival of competitiveness include processes such as the effectiveness of mechanisms that prevent the occurrence of damaging effects of water deficits (Burns, 2006).

The occurrence of various vessel types: short and long together with wide and narrow vessels in *Tithonia diversifolia* and *Chromolaena odorata* play an important role in water conservation and has reduced the vulnerability of the stem to cavitation. The wider the xylem pores, the more the ability to

conduct water through the conduit pit membrane, this function as support and strength to the stem during stress situation (Hacke et al., 2001). Wider vessels are more likely to be embolised and that the most well known mechanism for embolism recovery is replacement of embolised xylem vessels by new xylem vessel production. The presence of narrow and short vessels assist the invasive species during stress period, once the wider vessels are cavitated, the narrow and short vessels pick up the function of transport which prevents dieback in the invasive species. Vessels contribute to the reasons why angiosperms are the dominant land plant. They are able to continue active growth in the dry season, even in the savanna, when moisture availability becomes a limiting factor of growth and development (Jayeola, 2000).

The long coiled trichomes reported for both *Tithonia diversifolia* and *Chromolaena odorata* are also important xeromorphic features present in the invasive species. They are used by these plants to resist herbivory, herbivorous animals therefore avoid eating them because of the poisonous secondary metabolites stored in the trichomes. These coiled trichomes are effective in light piping, which is, concentrating light on the underlying tissues; alter heat loss from a plant. They reduce wind movement within the leaf and are useful in reducing water loss through transpiration, in water and mineral absorption (Dickinson, 2000).

The high stomata sizes recorded for the invasive species suggests a corresponding diffusion of carbon dioxide in and water vapour out of the leaf, this implies that the invasive species have higher growth rate than the non-invasive species as a consequence of higher photosynthetic capacity. The prolific amount of growth and reproduction in invasive plants may be achieved by greater net photosynthesis and/or resource-use efficiency (McDowell, 2002). The stomatal index (S.I.) is low in the invasive species. This reduces excessive evaporation that might lead to desiccation and an equally severe disruption of photosynthetic function.

Medullary rays are prominent in the invasives, they allow the radial transmission of sap and are essential in the process of

tylosis. The effective transport of nutrition between the core of the trunk and the outer parts enhance the invasiveness of the invasives.

The data recorded in this study are sufficient for delimiting the invasive species studied from the non invasive species in the family Asteraceae. The characters responsible for invasiveness in the invasive species are the presence of: large stomatal size, low stomatal index, coiled trichomes, more sclerenchyma cells, more parenchyma cells, large vessel diameter and prominent medullary rays.

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