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Herbaceous plants of the Amazon floodplain near Manaus: Species diversity and adaptations to the flood pulse

by

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Abstract

In the floodplain of the Amazon river near Manaus, 388 herbaceous plant species, excepting epiphytes, were collected belonging to 64 families and 182 genera. 330 species are considered terrestrial, 34 aquatic, the others have an intermediate status. Most of the species occur in relatively small numbers. Only 17 species formed large monospecific stands. The largest number of species (273) was found during the dry phase in disturbed areas on the levees, as for instance in abandoned fields, because of a reduced impact of the flood and high light intensity. Low numbers were recorded during low water period from the floor of floodplain forest (25) because of insufficient light conditions and from low lying lake beds (26), which were dominated by a few highly adapted species.

The following attributes were found to favour the occurrence of herbaceous plants in the Amazon floodplain: resistance of seeds and spores to flooding and dessication; short reproductive cycles; high reproduction rates; high primary production; tolerance of adult plants to flooding and drought; adaptations to waterlevel fluctuations (for example a floating way of life).

Short life cycles and high reproduction rates allow the quick colonization of disturbed habitats and the substitution of population losses (r-strategy). This strategy is supported by the elevated nutrient status of the Amazon river floodplain in comparison with the floodplain of the Negro River, where herbaceous plants are scarce. The number of ruderal species and weeds including a rising number of neophytes is large.

The great species diversity is related to great habitat diversity, fertility of sediments and water, predictability of the floodpulse and the reduction of interspecific competition due to the annual set back of the populations by the flooding and drought. The observations are in concordance with the predictions of the floodpulse concept.

Keywords: **Floodplain, Amazon river, herbaceous plants, species diversity, adaptations.**

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Introduction

Along its middle and lower course, the Amazon River is accompanied by a large fringing floodplain locally called *várzea*. The hydrograph is monomodal and rather predictable: maximum flood is reached in June/July, the lowest water level is found in October/November. Near Manaus, average amplitude of the flood pulse is about 10 m. Sediments deposited in the *várzea* are of Andean origin and belong to the most fertile soils in the Amazon basin. Levees are covered by a dense highly adapted floodplain forest, which can withstand on an average of up to 230 days of inundation (JUNK 1989). Lowlying and strongly disturbed areas are colonized by a luxuriously growing herbaceous vegetation, rich in species, which shows adaptations to the flood pulse.

Inspite of the abundance of herbaceous plants in the *várzea* and its importance to agriculture and husbandry, information about the species occurring in this area and its ecology is scarce. Available literature deals mainly with the species that frequently occur as weeds on cultivated fields (ALBUQUERQUE 1978; LORENZI 1982; ARANHA et al. 1982; LEITÃO FILHO et al. 1982) or plants growing in pastures (OHLY 1987). Until how, a check-list of species is lacking. The present paper provides information on the species that occur in the main habitats of the *várzea* and discusses adaptations to the flood pulse.

Material and methods

The herbaceous plants were studied for several years at various locations in the floodplain of the Amazon in a range of about 100 km which extended from upstream to downstream of Manaus. The study does not include the transition zone of the non-flooded *terra firme* rainforest. Epiphytes were not considered, because they are not subject to flood stress.

According to environmental conditions, six major habitats were distinguished:

- *várzea* lakes representing permanent or periodic aquatic habitats.
- floating islands of organic material representing palustric habitats with a stable water level.
- low-lying lake beds, exposed only during short periods of time, and influenced by little deposition of very fine sediments.
- areas of intensive sedimentation and long lasting floods.
- areas at higher elevations strongly distrubed by man or by natural events (wind, current, erosion).
- the floor of the inundation forest.

All of the collected specimens were pressed, dried, and labelled to show the site of collection, the abundance of the species at the site, and its mode of existence. From these data, approximate information on the location, frequency, and mode of existence was compiled. When occurrence and mode of existence were non-specific, several symbols were employed for a single species. It is not intended for use in establishing phytosociological units.

The material collected was lodged in the herbarium of Instituto Nacional de Pesquisas da Amazônia (INPA) at Manaus, Brazil. Taxonomic identification of the specimens was conducted in the herbarium of INPA. In case of doubt, duplicate specimens were sent to specialists by the curator of the herbarium to confirm the accuracy of the identification.

Results

Herbaceous plant species and their occurrence in the *várzea*

Alternating between a well-defined terrestrial phase and an aquatic phase results in the development of short-lived herbaceous plant communities, which subsequently colonize the same habitat during the terrestrial and the aquatic phases. Therefore it is useful to classify the species as either aquatic or terrestrial. However, in some cases such a classification is difficult, because many species show considerable adaptations on the complementary phase, permitting their survival in both phases. Many species depend upon the change between the aquatic and the terrestrial phases and would not occur, if the flood pulse was eliminated. Therefore it seems advisable to speak of a gradient, which extends over the spectrum from exclusively aquatic to purely terrestrial species. Table 1 indicates the species and gives information about their frequency, mode of existence and principle habitats.

Table 1: Herbs, grasses, and sedges from various habitats in the *várzea* of the Amazon River near Manaus.

Frequency (F): 1 - rare, 2 - widely distributed, 3 - common, 4 - forms monospecific stands, 5 - dominant over large areas.
Mode of existence (M): a - aquatic, b - aquatic with a terrestrial phase, p - palustric, t - terrestrial; t* - terrestrial, but survives periods of submergence, v - vine.
Principle habitats (H): A - *várzea* lakes, B - floating islands, C - low-lying lake beds, C* - moist depressions, D - areas of intensive sedimentation; E - disturbed areas at higher elevations, F - inundation forest.

FAMILY/SPECIES	F	M	H
Acanthaceae			
Justicia comata LAM	3	t	E
J. laevilinguis LINDAU	2	a	A
Stethoma cf. *pectoralis* (JACP.) RAF.	2	t	E
Alismataceae			
Sagittaria sprucei MICHELI	2	p	C*
Amaranthaceae			
Alternanthera brasiliana, var. *villosa* R.E. FRIES.	4	t	E
A. hassleriana CHOD.	1	a	A
A. paronichoides ST. HIL.	2	t	D
A. pilosa MOQ.	4	t	C D E
A. tenella COLLA	1	t	E
Althernanthera sp.	1	t	E
Amaranthus spinosus L.	2	t	E
A. viridis L.	2	t	D E
Chamissoa altissima H.B.K.	1	t	E
Apiaceae			
Hydrocotyle sp.	1	p	B
Apocynaceae			
Rhabdadenia macrostoma (BENTH) M. ARG.	2	t v	B E
Rhabdadenia sp.	1	t v	B E
Odontadenia nitida (VAHL) M. ARG.	2	t v	E

FAMILY/SPECIES	F	M	H
Aracea			
Montrichardia arborescens SCHOTT	4	b p	B C*
Pistia stratiotes L.	4	a	A
Asclepiadaceae			
Madanosperma sp.	2	t v	E
Matelea sp.	2	t v	E
Begoniaceae			
Begonia sp.	1	t	B
Boraginaceae			
Heliotropium cf. *filiforme* H.B.K.	2	t	C D E
H. indicum L.	2	t	C D E
H. procumbens H.B.K.	1	t	C D E
Campanulaceae			
Sphenoclea zeylanica GAERTN.	3	t	D
Capparaceae = Capparidaceae			
Cleome spinosa JACQ.	1	t	D
Ceratophyllaceae			
Ceratophyllum demersum L.	2	a	A
Ceratopteridaceae			
Ceratopteris pteridoides UNDERW.	3	a	A
Chenopodiaceae			
Chenopodium ambrosioides BERT. ex. STEUD.	2	t	D
Commelinaceae			
Aneilema umbrosum (VAHL.) KUNTH.	1	t	E
Commelina erecta CHAPM.	3	t	B
Commelina sp.	2	t	E
Compositae = Asteraceae			
Acanthospermum hispidum DC.	2	t	D
Ageratum sp.	2	t	D E
Ambrosia artemisiaefolia L.	3	t	E
Centratherum sp.	2	t	E
Compositae = Asteraceae			
Conyza bonariensis (L.) CRONQUIST.	1	t	E
C. floribunda H.B.K.	1	t	E
Conyza sp.	1	t	E
Eclipta alba HASSK.	3	t	C D E
Egletes viscosa LESS.	2	t	D E
Emilia sonchifolia DC.	1	t	B E
Erechtites hieracifolia RAFIN. ex. DC.	1	t	B E
Eupatorium candolleanum HOOK. et. ARN	1	t	B E
Gymnocoronis spilanthoides, var. *subcordata* (DC.) BAKER	1	t	B D
Mikania congesta DC.	3	t	B E
M. cordifolia WILLD.	2	t	B E
Mikania sp.	2	t	B E
Pacourina edulis AUBL.	1	t	C E
Spilanthes acmella DC.	1	t	E
Spilanthes sp.	2	t	E
Trichospira menthoides H.B.K.	1	t	E
Wedelia paludosa DC.	3	t	E

FAMILY/SPECIES	F	M	H
W. scaberrima BENTH.	3	t	E
W. trilobata A.S. HITCH.	2	t	E
Wedelia sp.	2	t	E
Wulffia baccata O. KUNTZE	2	t	E
W. stenoglossa DC.	2	t	E
Wulffia sp.	2	t	E
Convolvulaceae			
Ipomoea alba L.	2	t v	E
I. aquatica FORSK.	2	a v	A
I. ascorifolia ROEM et SCHULT.	2	t v	E
I. carnea JACQ. subsp. *fistulosa* (MART. ex CHOYSY) D. AUSTIN	3	t	E
I. phillomega HOUSE	2	t v	E
I. quamoclit L.	2	t v	E
I. setifera POIR	3	t v	B E
I. squamosa CHOISY in DC.	2	t v	B E
I. umbellata C.F.W. MEYER	2	t v	B E
Ipomoea sp.	2	t v	E
Operculina alata (HAM.) URB.	2	t v	E
Operculina sp.	2	t v	E
Prevostea umbellata CHOISY	1	t v	E
Tetralocularia pennellii O'DONELL	2	t v	E
Costaceae Zingiberaceae			
Costus arabicus L.	2	t	F
Cucurbitaceae			
Elaterium amazonicum MART.	2	t v	E
Elaterium sp.	2	t v	E
Gurania cissoides COGN.	1	t v	E
G. tricuspidata COGN.	1	t v	E
Gurania sp.	1	t v	E
Luffa operculata COGN. in MART.	2	t v	E
Melothria sp.	2	t v	E
Momordica charantia L.	2	t v	E
Cyperaceae			
Bulbostylis capillaris C.B. CLARKE	3	t	D
Bulbostylis sp.	2	t	D
Cyperus compressus L.	2	t	D E
C. diffusus VAHL.	1	t	E
C. distans L.	2	t	E
C. esculentus L.	3	t	C
C. ferax L.C. RICH.	3	t	D
C. flavus BOECK.	2	t	D
C. haspan L.	3	t	D
C. imbricatus RETZ	3	t	D
C. laetus F. & C. PRESL.	3	t	D
C. ligularis L.	3	t	D
C. luzulae (L.) RETZ.	2	t	E
C. meyerianus KUNTH.	2	t	D
C. mutusii (H.B.K.) GRISEB.	1	t	D
C. radiatus VAHL.	2	t	D

FAMILY/SPECIES	F	M	H
C. rotundus BENTH.	3	t	C D E
C. sphacelatus ROTTB.	2	t	E
C. surinamensis ROTTB.	3	t	D E
C. unicolor BOECK.	2	t	D E
Cyperus sp.	1	t	D
Eleocharis variegata PRESL.	2	p	B
Fimbristylis argentea VAHL.	2	t	D
F. dichotoma (L.) VAHL.	2	t	D
F. miliacea (L.) VAHL.	3	t	D
F. spadicea (L.) VAHL.	2	t	D
Kylinga pumila MICHX.	2	t	D
Rhynchospora ciliata KÜKENTH.	2	t	D
R. corymbosa (L.) BRITTON.	2	p	B
R. schomburgkiana (CLARKE.) T. KOYAMA	2	p	B
Scirpus cubensis POEPP. & KUNTH.	4	a	A B
Scleria cf. *microcarpa* NEES.	2	t	E F
S. pterota PRESL.	2	t	E
S. secans (L.) URB.	2	t v	E
S. uleana BOECK.	2	t	F
Scleria sp.	2	t	E
Torulinium odoratum (L.) HOOPER	3	t	D
Dioscoreaceae			
Dioscorea marginata GRISEB.	1	t v	E
Dioscorea sp.	1	t v	E
Euphorbiaceae			
Acalypha arvensis POEPP. & ENDL.	2	t	E
A. poirettii SPRENG.	2	t	E
Acalypha sp.	1	t	E
Caperonia castanaeifolia (L.) ST. HILL.	3	t	E
Croton chamaedryfolius GRISEB.	2	t	D E
C. lobatus L.	2	t	E
C. miquelensis FERGUSON.	2	t	E
C. trinitatis MILLSP.	1	t	E
Croton sp.	1	t	E
Dalechampia scandens VELL.	1	t v	E
D. tiliaefolia LAM.	1	t v	E
Dalechampia sp.	1	t v	E
Euphorbia brasiliensis LAM.	1	t	E
E. hirta L.	1	t	E
E. pilulifera L.	2	t	D E
E. thymifolia L.	2	t	D E
Euphorbia sp.	2	t	D E
Phyllanthus fluitans BENTH. ex MÜLL.	2	a	A
P. niruri L.	2	t	D E
P. stipulatus (RAF.) WEBSTER.	1	t	E
Gentianaceae			
Coutobea ramosa AUBL.	1	t	E
Gramineae = Poaceae			
Acroceras cf. *zizanioides* (H.B.K.) DANDY	3	t	E
Andropogon bicornis L.	1	t	B

FAMILY/SPECIES	F	M	H
Andropogon sp.	2	t	E
Brachiaria fasciculata (SWARTZ.) PARODI	2	t	E
B. mutica (FORSK.) STAPF	3	t	E
Coix lachryma JOBI L.	1	t	E
Cynodon dactylon (L.) PERS.	5	t*	D E
Digitaria ciliaris (RETZ.) KAEL.	3	t	D E
D. horizontalis WILLD.	3	t	D E
D. sanguinalis SCOP.	3	t	D E
D. violascens LINK	3	t	E
Echinochloa cruspavonis (L.) BEAUV.	1	b p	D
E. polystachya (H.B.K.) HITCH.	5	b	A C D E
Echinochloa sp.	1	t	E
Eleusine indica (L.) GAERTN.	3	t	D E
Eragrostis amabilis (L.) WIGHT. & ARN.	2	t	D
E. ciliaris (L.) R. Br.	2	t	E
E. glomerata L.H. DAWEY.	3	t	D E
E. hypnoides (LAM.) R. et. P.	2	t	D
Gramineae = Poaceae			
E. reptans NEES.	2	t	D
Eriochloa punctata (HAM.)	2	t	E
Gynerium sagittatum BEAUV.	3	t	D E
Homolepis aturensis (H.B.K.) CHASE.	2	t	E
Hymenachne amplexicaulis (RUDGE.) NEES	4	b	A C D E
H. donacifolia (RADDI.) CHASE.	1	b	D
Isachne polygonoides DOELL.	3	t	B E
Isachne sp.	2	t	E
Lasiacis procerrima (HACK.) HITCH.	1	t	E
Leersia hexandra SWARTZ.	4	b p	A B C*
Leptochloa domingensis (JACQ.) TRIND.	2	t	D E
L. scabra NEES.	3	t	D E
L. virgata (L.) BEAUV.	3	t	D E
Luziola spruceana BENTH.	3	b	A C
Oryza grandiglumis (DOELL.) PROD.	3	b	A C E F
O. perennis MOENCH.	5	b	A C E
Panicum bolivieense HACK.	3	t	E
P. chloroticum NEES.	3	b	C E
P. dichotomiflorum MICHX.	3	t	E
P. elephantipes NEES.	1	b	C
P. laxum SW.	2	t	E
P. maximum JACQ.	2	t	E
P. mertensis ROTH.	1	t	E
P. micranthum H.B.K.	2	t	D E
P. pilosum SW.	3	t	E
Panicum sp.	2	t	E
Paspalum amazonicum TRIND.	2	t	E
P. conjugatum BERG.	4	t	E
P. fasciculatum WILLD. ex. FLUEGGE	5	t*	D E
P. melanospermum DESV. ex. POIR.	2	t	D E
P. orbiculatum POIR.	2	t	E
P. repens BERG.	5	a b	A C D

FAMILY/SPECIES	F	M	H
Paspalum sp.	2	t	E
Pennisetum hirsutum NEES	2	t	E
Pennisetum purpureum SCHUM	2	t	E
Raddiella esenbeckii (STEUD.) CELDERON & SODERSTROM	1	t	E
Reimarochloa brasiliensis (SPRENG.) HITCH.	3	i	D
Reimarochloa sp.	1	t	D
Setaria geniculata (LAM.) BEAUV.	2	t	E
Sorghum arundinaceum (WILLD.) STAPF.	4	t	E
Spartina brasiliensis RADDI	2	t	E
Heliconiaceae = Musaceae			
Heliconia cf. *marginata* (GRIGGS.) PITT	3	t	F
H. striata HORT.	3	t	F
Hydrocharitaceae			
Limnobium laevigatum (HUMB. and BONPL. ex. WILLD.) HEINE	2	a	A
Limnobium sp.	2	a	A
Hypnaceae			
Vesicularia amphibola (SPRUCE.) BROTH.	1	p	B
Labiatae = Lamiaceae			
Hyptis brevipes BENTH.	2	t	E
H. lantanaefolium POIT.	2	t	E
H. mutabilis BRIG.	2	t	E
H. parkeri BENTH.	2	t	E
H. recurvata POIT.	2	t	E
Hyptis sp.	2	t	E
Ocimum canum SIMS.	2	t	E
O. micranthum BENTH.	2	t	E
Leguminosae			
(Leg. Caesalpinoidea):			
Cassia nictitans var. *disadena* (STEUD.)	2	t	D E
Cassia obtusifolia L.	3	t	E
C. occidentalis L.	2	t	D
(Leg. Mimosoidea):			
Mimosa dormiens HUMB. & BONPL.	3	t	E
M. insidiosa BENTH.	3	t	E
M. invisa MART.	2	t	E
M. pigra L.	3	t	E
M. polycarpa KUNTH.	2	t	E
Mimosa sp.	2	t	E
Neptunia oleracea LOUR.	3	a	A
(Leg. Papilionoidea = Fabaceae):			
Aeschynomene rudis BENTH.	2	b	B
A. sensitiva SW. var. *amazonica* RUDD.	3	t	B C D
Aeschynomene sp.	3	t	C D
Arachis sp.	1	t	E
Centrosema sp.	2	t v	E
Clitoria falcata LAM. var. *falcata*	1	t v	E
Crotalaria anagyroides H.B.K.	2	t	E
C. nitens H.B.K.	1	t	E

FAMILY/SPECIES	F	M	H
C. pallida AIT.	2	t	E
Cymbosema roseum BENTH.	1	t v	E
Idigofera suffruticosa MILL.	1	t	E
Neptunia oleracea LOUR.	3	a	A
Phaseolus campestris MART.	2	t v	E F
P. ovatus BENTH.	2	t v	E
P. pilosus H.B.K.	2	t v	E
Phaseolus sp.	2	t v	E
Rhynchosia minima (L.) DC.	2	t v	E
Rhynchosia sp.	2	t v	E
Sesbania exasperata H.B.K.	2	t	D E
Teramnus volubilis SW.	2	t v	E
Vigna sp.	1	t v	E
Lemnaceae			
Lemna aequinatialis WELW.	2	a	A
L. valdiviana PHIL.	2	a	A
Spirodela intermedia W. KOCH.	2	a	A
Wolffiella neotropica E. LANDOLT.	2	a	A
W. lingulata HEGELM.	2	a	A
W. oblonga HEGELM.	2	a	A
Lentibulariaceae			
Utricularia foliosa L.	3	a	A
U. gibba L.	2	a	A
Utricularia sp.	1	a	A
Limnocharitaceae			
Limnocharis flava BUCH. var. *flava*	1	p	C*
Loganiaceae			
Spigelia anthelmia L.	1	t	E
Loranthaceae			
Phoradendron platycaulon EICHL.	1	t	E
Lythraceae			
Couphea melvilla LINDLEY	1	t	B E
Malvaceae			
Hibiscus abelmoschus (MEDIK.) DC.	1	t	B E
H. dimidiatus SCHRANK.	1	t	B E
H. furcatus WILLD.	1	t	B E
H. furcellatus LAM.	1	t	B E
H. sororius L.	1	t	B E
Malachra radiata L.	1	t	E
Pavonia paniculata CAV. var. *corymbosa* GÜRKE.	1	t	B E
Sida acuta BURM. var. *obidensis* H. MONTEIRO	2	t	E
S. rhombifolia L. var. *canariensis* (WILLD.) K. SCHUM.	2	t	E
S. setosa COLLA.	2	t	E
S. surinamensis MIQ.	1	t	E
Sida sp.	1	t	E
Urena cf. *lobata* L. var. *reticulata* GÜRKE.	1	t	E
Malpighiaceae			
Stigmatophyllum sp.	1	t v	E

FAMILY/SPECIES	F	M	H
Marantaceae			
Calathea cf. *capitata* LINDL.	3	t	F
C. comosa K. SCHUM.	3	t	F
C. lanata PETERS.	1	t	F
C. cf. *loeseneri* MACBR.	2	t	F
C. luba (AUBL.) MEYER.	1	t	F
C. micans (MART.) KOERN.	1	t	F
Calathea sp.	2	t	F
Ischnosiphon polyphyllus (P. & F.) KOERN.	1	t	F
Marantha sp.	2	t	F
Thalia geniculata LINN.	1	b p	C*
Marsiliaceae			
Marsilea polycarpa HOOK & GREV.	3	a	A
Melastomataceae			
Aciotis aequatorialis COGN.	2	t	E
A. amazonica COGN. var. *radicans* COGN. ex. CHAR.	2	t	E
Aciotis sp.	2	t	E
Menispermaceae			
Cissampelos andromorpha DC.	2	t v	E
C. glaberrima ST. HIL.	1	t v	E
Cissampelos sp.	1	t v	E
Odontocarya arifolia BARNEBY.	2	t v	E
O. tamoides (DC.) MIERS.	2	t v	E
Nymphaeaceae			
Nymphaea blanda G.F.W. MEYER	1	a	A
Victoria amazonica SOWERBY	3	a	A
Onagraceae = Oenotheraceae			
Ludwigia octovalvis (JACQ.) RAVEN	2	t	D
L. affinis (DC.) H. HARA	2	p t	B D
L. decurrens WALT.	3	t	D
L. densiflora (MICHELI.) H. HARA	4	t	D
L. elegans (CAMB.) H. HARA	2	t	D
L. helminthorrhiza (MART.) H. HARA = *L. natans* HUMB. & BONPL.	3	a	A
L. leptocarpa (NUTT.) H. HARA	2	p t	D
L. lithospermifolia (MICHELI.) H. HARA	2	t	D E
L. octovalvis (JACQ.) RAVEN.	2	t	D
L. rigida (MIQ.) SANDWITH.	2	t	D
Ludwigia sp.	2	t	D E
Orchidaceae			
Eulophia alta (L.) FAWE & RENDL.	1	p	B
Oxalidaceae			
Oxalis barrelieri L.	1	t	E
Oxalis sp.	1	t	E
Parkeriaceae			
Ceratopteris pteridoides UNDEW.	3	a	A
Passifloraceae			
Passiflora organensis GARDN.	1	t v	E
P. vespertilio L.	1	t v	E
Passiflora sp.		t v	E

FAMILY/SPECIES	F	M	H
Pedaliaceae			
Sesamum indicum L.	1	t	E
Phytolaccaceae			
Microtea debilis SWARTZ.	1	t	E
Piperaceae			
Peperomia pellucida (L.) H.B.K.	3	t	E F
Peperomia sp.	2	t	E F
Piper aduncum LINN. var. *aduncum*	2	t	E F
P. hispidum H.B.K. var. *hispidum*	3	t	E F
P. malacophyllum (PRESL.) C. DC.	2	t	E F
P. striatipetiolatum YUM.	2	t	E F
Piper sp.	1	t	E F
Pothomorphe peltata (L.) MIG.	1	t	E F
Polygonaceae			
Polygonum acuminatum H.B.K.	3	b	C E
P. spectabile MART.	3	b	C E
Polypodiaceae			
Lindsaya sp.	1	t	F
Nephrolepis biserrata (SW.) SCHOTT.	1	p t	B
Pityrogramma calomelanos (L.) LINK.	1	p t	B
Thelypteris serrata (CAV.) ALSTON.	2	p t	B
T. totta (TUMB.) SCHELPE.	2	p t	B
Thelypteris sp.	1	p t	B
Pontederiaceae			
Eichhornia azurea (SW.) KNUTH.	1	a	A
E. crassipes (MART.) SOLMS.	4	a	A
Pontederia rotundifolia (L.F.) CASTELL.	3	a p	A C*
Portulacaceae			
Portulaca oleracea L.	3	t	D E
Talinum paniculatum (JACQ.) GAERTN.	1	t	E
Ricciaceae			
Ricciocarpus natans (L.) CORDA.	2	a	A
Rubiaceae			
Borreria capitata var. *tenella* (H.B.K.)	2	t	D E
B. laevis (LAM.) GRISEB.	2	t	E
B. verticillata (L.) G.F.W. MEYER	2	t	E
Borreria sp.	2	t	E
Diodia kuntzei K. SCHUM.	2	t	E
D. ocimifolia (WILLD.) BREM.	2	t	E
Hedyotis corymbosa (L.) LAM.	2	t	D E
H. cf. *herbacea* L.	2	t	D E
Mitracarpum hirtum DC.	2	t	E
Mitracarpum sp.	2	t	E
Oldenlandia corymbosa L.	2	t	D E
O. lancifolia (DC.) SCHUM.	2	t	D E
Palicourea marcgravii ST. HILL.	2	t	E
Salvinaceae			
Azolla cf. *microphylla* KAULF.	3	a	A
Salvinia auriculata AUBL.	4	a	A
S. minima BAKER.	3	a	A

FAMILY/SPECIES	F	M	H
S. sprucei KUHN in MART.	2	a	A
Sapindaceae			
Cardiospermum halicacabum L.	2	t v	E
Paullinia stipularis BENTH. ex. RADLK.	1	t v	E
Scrophulariaceae			
Alectra brasiliensis BENTH.	1	t	E
Lindernia crustacea (L.) F. VON MUELL.	3	t	D E
L. diffusa (L.) WETTST.	3	t	D E
Lindernia sp.	2	t	D E
Mecardonia procumbens (MILL.) SMALL	2	t	D E
Scoparia dulcis L.	3	t	E
Stemodia sp.	1	t	E
Torenia sp.	2	t	D E
Solanaceae			
Physalis angulata L.	2	t	E
Physalis sp.	2	t	E
Solanum anceps RUIZ. & PAV.	1	t	E
S. arborescens HUMB. & BONPL.	1	t	E
S. cf. *crinitum* LAM.	2	t	E
S. jamaicense MILL.	2	t	E
S. kidniotrichum BITT.	1	t	E
S. nigrum L. - *Solanum americanum* MILL.	3	t	E
S. nodiflorum JACQ.	2	t	E
S. sisymbriifolium LAM.	1	t	E
S. thelopodium SENDT. in MART.	1	t	E
Solanum sp.	1	t	E
Turneraceae			
Piriqueta cistoides G.F.W. MEYER.	2	t	D E
Urticaceae			
Urera sp.	1	t	E
Verbenaceae			
Lantana camara L.	1	t	E
L. canescens H.B.K.	2	t	E
L. rodonensis MOLDENKE	1	t	E
Phyla betulaefolia (H.B.K.) GREENE.	2	t	D E
Stachytarpheta elatior SCHRAD. ex SCHULT.	2	t	E
Vitex cymosa BERT. ex SPRENG.	1	t	E
Vitaceae			
Cissus erosa L.C. RICH.	2	t v	B E
C. gongylodes BURCH. ex BAKER.	2	t v	B E
C. sicyoides L.	1	t v	B E
Cissus sp.	2	t v	B E

A total of 388 species were identified. They belong to 64 families and 182 genera The best represented family is the Gramineae with 60 species. In second place is the Cyperaceae with 37 species, followed by the Leguminosae with 30 and the Compositae with 27 species. A total of 42 families were represented by one to three species. The total number in the region investigated is about 10 % to 20 % greater than the value reported here. This discrepancy is accounted for by plants that occur in isolated locations only. In sites at the highest elevations, which are subject to flooding at intervals of several years and in areas used for agriculture, the occurrence of unreported species can be expected.

The classification of herbs according to their modes of existence showed that 330 species, or 85 % of the total, are terrestrial. There are 34 aquatic species, which is 9 % of the total, while only 20 species, or 5 %, are considered to be palustric. Aquatic species with terrestrial phases number 17 and account for 4 % of the total. The main growth period of two of them, *Cynodon dactylon* and *Paspalum fasciculatum*, is during the terrestrial phase, but they can survive for many months with their stems under water (Table 2).

Table 2: Classification of herbs acording to frequency (F) of occurrence, principle habitats (H), and mode of existence (M). For explanation of symbols see Table 1. Many species show a wide range of mode of existence and habitat preferences. Therefore total of these categories are greater than total species numbers.

Frequency		**Mode of existence**		**Principle habitats**	
F	**n**	**M**	**n**	**H**	**n**
1	110	a	34	A	42
2	189	b	17	B	44
3	72	p	20	C	26
4	12	t	330	D	92
5	5	v	58	E	273
				F	25

The classification according to the main sites of occurrence shows that 273 terrestrial species, or 71% of the total prefer disturbed locations at higher elevations. A total of 92 species, or 24 % of the total, are characteristic of areas of fresh sediment deposition, but isolated individuals can also settle on sites at higher elevations. The low-lying beds of lakes are preferred by 26 species, 7 %, and the inundation forest supports 25 species, 7 %. Bays of the *várzea* lakes with standing water are colonized by 42 species, 11 % of the total, during the aquatic phase, while 44 species, 11 %, inhabit the floating islands.

An analysis of species abundance shows that the great majority of them occur in relatively small numbers. The frequency values of 1, 2, or 3 were assigned to 110 or 29 %; 189 or 49 %, and 72 species or 18 % of the total, respectively. Only 12 species, or 3 % or the total, were very abundant, and 5 were so dominant that they were frequently able to form large, monospecific stands. Of the 17 very abundant, dominant species, four are classified in the category of aquatic macrophytes: *Pistia stratiotes, Scirpus cubensis, Eichhornia crassipes*, and *Salvinia auriculata*. Six species are aquatic with a clearly evident terrestrial phase: *Echinochloa polystachya, Hymenachne amplexicaulis, Leersia hexandra, Oryza perennis, Paspalum repens*, and *Montrichardia* *arborescens. M. arborescens* is also classified as a swamp-dwelling plant. Two species are terrestrial but can survive for long periods of time with their stems submerged: *Cynodon dactylon* and *Paspalum fasciculatum.* Five species are purely terrestrial: *Alternanthera pilosa, A. brasiliana, Paspalum conjugatum, Ludwigia densiflora,* and *Sorghum arundinaceum.*

Adaptations to the flood pulse

The following attributs are common to herbaceous plant species that grow in the *várzea*:

- Resistance of seeds and spores to flooding and desiccation
- Short reproductive cycles and high reproduction rates
- High productivity
- Tolerance of plants to flooding
- Tolerance of plants to desiccation
- Adaptations to water level fluctuations

In most cases, the resistance of seeds and spores to flooding is a preadaptation rather than an adaptation, as shown by the many ruderal species, which colonize the floodplain. An adaptation is found in *Ludwigia densiflora,* which maintains the seeds in woody seed sapsules during the flood period and releases them when the habitat is dry again. This species seems to be restricted to the *várzea.* Germination of diaspores of most aquatic species occurs during the dry period only.

The seed-bank in the sediment is very large. On the sediments of drying lakes up to 10,000 seedlings per m^2 were counted. On newly formed sediment bars in the middle of the river 10 to 100 seedlings per m^2 were observed.

Short life cycles and high reproduction rates are essential for the colonization of ephemeral habitats in the floodplain. Many small annual species already produce seeds after a period of four weeks. Tall ones, which grow 2.5 m high e.g. *Ludwigia densiflora* need 2-3 months. Number of seeds is very high, e.g. *Paspalum conjugatum* 1,500, *Eleusine indica* up to 135,000, *Portulaca oleracea* 10,000 (HOLM et al. 1977). In aquatic macrophytes, vegetative propagation is very effective, e.g. by fragmentation (*Salvinia* spp., *Ricciocarpus natans, Lemna* spp., *Ceratophyllum demersum, Echinochloa polystachya*), by runners (*Eichhornia crassipes, Pistia stratiotes, Limnobium stoloniferum*) and by frond buds (*Ceratopteris pteridioides*).

High rates of primary production are necessary to compensate for great annual losses in an unstable environment. The herbaceous plant communities of the *várzea* belong to the most productive ones in the world. Short living, annual terrestrial communities produce between 6 to 16 t ha^{-1} dry biomass within three months. Highly adapted perennial species e.g. *Paspalum fasciculatum* produce 72 t ha^{-1} during a nine month growth period and *Echinochloa polystachya* produce more than 100 t ha^{-1} a^{-1} (JUNK & HOWARD-WILLIAMS 1984; JUNK 1986; JUNK & PIEDADE 1993; PIEDADE et al. 1991).

Various morphological peculiarities can be interpreted as adaptations to flooding, e.g. facultative formation of aerenchyma in the roots and stems (many of the *Ludwigia* species, *Neptunia oleracea, Sesbania exasperata, Sphenoclea ceylanica*), the blisterlike swellings of submersed stems (*Caperonia castaneifolia, Polygonum tomentosum*) and the development of pneumatophores (*Phaseolus* cf. *longifolius, Ludwigia affinis* and other *Ludwigia* species). The stems of *Paspalum fasciculatum* and *Cynodon dactylon* survive below water.

Many aquatic species show astounding morphological and physiological plasticity to survive the terrestrial phase. Free floating species, such as *Eichhornia crassipes, Pontederia rotundifolia, Ludwigia natans, Neptunia oleracea*, and *Paspalum repens*, show reductions in size, the area of their leaf surfaces, water content, and, in the cases of *Ludwigia* and *Neptunia* species, the amounts of aerenchymatic tissue in the roots and stems when growing on land. The leaves of *Paspalum repens*, become more hairy. The rhizomes of *Victoria amazonica* and *Nymphaea blanda* survive in moist sediments.

During the aquatic phase, large fluctuations in water level and low transparency of the water require adaptations to maintain the organs of photosynthesis just below or above the water surface. The majority of aquatic macrophytes have adapted to a free floating way of life. All species rooted in the sediment have emergent or floating leaves.

Discussion

With 64 families, 182 genera, and 388 species, excluding epiphytes, the herbaceous vegetation in the central part of the *várzea* near Manaus is astoundingly rich. In contrast, there are about 350 tree species in the inundation forest. If the epiphytes and the species occurring in the border region of the terra firma were also counted, the total number of higher plant species would number about 1000. Of these, about 450 are shrubs and trees and 550 are herbaceous species. In the Bolivian lowlands, BECK (1983) found about 400 plant species, including trees. The flora of the savannas in Humaitá, where about 40 % of the area is periodically flooded during the rainy season, encompasses 314 species from the open grasslands, 151 species of the sparcely scattered patches of shrub growth, and 67 ruderal species (JANSSEN 1986). SEIDENSCHWARZ (1986) reported 245 species of herbaceous plants from the open areas of the river banks along the Rio Yuyapichis and Rio Pachitea and on the nearby areas of newly cultivated fields and roadsides in the tropical lowlands of Peru.

The great species diversity is in part a result of great habitat diversity. There is a gradient from permanently aquatic to nearly permanently terrestrial conditions. Furthermore, there is a patchy distribution of soils of different grain size. Sand dunes may alternate with silt depositions, waterlogged soils alternate with water deficient ones. Annual variability in local precipitation at the beginning of the dry period has a very strong effect on the seedling establishment and leads to great interannual variability in the community structure of annual herbaceous plants.

However, by examining the distribution of the herbaceous plants that occur in the *várzea*, we find that the great majority of terrestrial species, 273 or 71 % of the total, prefer distrubed locations at high elevations which are flooded for a short time during the average year but often remain dry for several years in a row. The total number of species is even greater because most of the species that prefer to settle in low-lying habitats also occur there occasionally. However, these areas are normally occupied by the floodplain forest which is colonized by only 25 herbaceous plant species, which account for 7 % of the total number in the region, because of insufficient light. An increase in the number of herbaceous species after clearing of the forest and the immigration of ruderal species onto the river banks was observed by SEIDENSCHWARZ (1986) at two areas he investigated in the Peruvian lowlands. Many of these species are ruderal plants and weeds, which are not confined to the *várzea* (CHASE 1944; HOLM et al. 1977, 1979; LORENZI 1982; LEITÃO FILHO et al. 1982; ARANHA et al. 1982). Among them are a group of neophytic weeds (Table 3).

Table 3: Important weeds in the *várzea* of the Amazon River and their regions of origin.

NAME	REGION OF ORIGIN	DISTRIBUTION
Primarily terrestrial:		
Cyperus rotundus	India	Primarily the tropics and subtropics worldwide
Cyperus esculentus	?	Primarily the tropics and subtropics worldwide
Fimbristylis miliacea	Tropical America	Moist tropics, worldwide
Fimbristylis dichotoma	Tropical America	Moist tropics, worldwide
Cynodon dactylon	Africa or Indo-Malaysia	Primarily the tropics and subtropics worldwide
Eleusine indica	Probably Southeast Asia	Primarily the tropics and subtropics worldwide
Paspalum conjugatum	Tropical America	Moist tropics, worldwide
Panicum maximum	Africa	Tropics and substropics, worldwide
Brachiaria mutica (*Panicum purpurascens*)	Tropical Africa	Moist tropics and subtropics, worldwide
Pennisetum purpureum	Tropical Africa	Tropics and subtropics, worldwide
Portulaca oleracea	North Africa or Europe	Worldwide except for high northern latitudes
Digitaria sanguinalis	Europe	Worldwide except for high northern latitudes
Amaranthus spinosus	Tropical America	Tropics and subtropics, worldwide
Heliotropium indicum	Paleotropical	Tropics, worldwide
Lantana camara	Tropical America	Tropics and subtropics, worldwide
Sida acuta	Central America	Tropics, worldwide
Solanum nigrum	Europe	Worldwide
Sphenoclea zeylanica	Tropical Africa	Tropics, worldwide except Australia
Primarily aquatic:		
Ceratophyllum demersum	Unknown	Worldwide
Pistia stratiotes	Unknown	Tropics and subtropics, worldwide
Salvinia auriculata	Tropical South America	Tropics, worldwide
Eichhornia crassipes	Tropical South America	Tropics, worldwide
Leersia hexandra	Tropical America	Tropics and subtropics, worldwide

Many of the adaptations shown by herbaceous plants in the *várzea* point to the need for quick growth, early maturity and high reproduction rates by seeds or by vegetative propagation. These mechanisms are characteristic of pioneer plants colonizing frequently disturbed areas, generally considered r-strategists. Flood-resistant seeds are the main prerequisite for the great number of weeds and ruderal species for a successful establishment in the *várzea*.

However, the predictability of the flood pattern allows for development of adaptations to the change between the terrestrial and aquatic phases. The aquatic and semi-aquatic grasses *Oryza* spp., *Luziola spruceana, Echinochloa polystachya, Hymenachne amplexicaulis, Paspalum repens*, and *Paspalum fasciculatum* belong to the group of adapted species. They accomplish specific parts of their life cycles during the terrestrial and the aquatic phases. Because of these adaptations they are quantitatively dominant along the middle and lower Amazon River. However, they have not been reported in habitats outside the floodplain. They do not occur along the upper reaches of the river and its small tributaries, because these habitats are subject to rapid, unpredictable flood pulses.

Quick growth and great primary production of adapted species can, in the long run, lead to strong interspecific competition and exclusion of other species. In the *várzea* this is not the case, because the perturbation caused by the flood pulse leads annually to a set-back in the community development, avoids the elimination of species by interspecific competition and maintains the system at a low seral stage.

With the periodic losses caused by the flood pulse and associated factors (e.g. current, sedimentation, erosion), a dense herbaceous vegetation can only be established over the long term when sufficient nutrients are present to permit a replacement of the losses. This is the case in the *várzea* of the Amazon River, but not in the neighbouring floodplain of the nutrient poor Negro River as shown by the sparcity of the herbaceous vegetation (JUNK 1983).

These findings agree with the predictions of the flood pulse concept (JUNK et al. 1989) that predictability of inundation, great habitat diversity, low interspecific concurrence and good nutrient supply allow a great number of species to colonize the *várzea* inspite of the heavy stress caused by the periodic changes between aquatic and terrestrial phases.

Resumo

Na área alagável (várzea) do rio Amazonas, perto de Manaus, foi encontrado um total de 388 espécies de plantas herbáceas não epífitas, pertencentes a 64 famílias e 182 gêneros. Destas, 330 espécies são consideradas terrestres, 34 aquáticas, e as restantes ocupam categorias intermediárias. Somente 17 espécies formam grandes populações monoespecíficas, enquanto que a maioria ocorre em baixas densidades. O maior número de espécies (273) foi encontrado durante a seca nas porções elevadas da planície inundável em áreas pertubadas, tais como plantios abandonados, onde a insolação é grande devido ao desmatamento, e o impacto da inundação é relativamente pequeno. Um reduzido número de espécies (25) foi encontrado no solo da mata inundável devido aos baixos índices de insolação, e no fundo seco dos lagos (26), que se encontra coberto por poucas espécies bem adaptadas.

Os seguintes fatores foram considerados como favoráveis à occorência de plantas herbáceas na várzea do Rio Amazonas: resistência das sementes e esporos contra a inundação e seca; ciclos reprodutivos curtos; altas taxas de reprodução; alta produção primária; tolerância de plantas adultas à inundação e seca; adaptações às flutuações de nível da água como, por exemplo o hábito de vida flutuante.

Os ciclos de vida curtos e as altas taxas de reprodução permitem a colonização rápida de áreas perturbadas e a reposição de perdas populacionais (estratégia-r). Esta estratégia é favorecida pelo elevado estatus de nutrientes da várzea do Rio Amazonas em comparação com a área alagável do Rio Negro (igapó), aonde plantas herbáceas ocorrem em número reduzido. O número de plantas ruderais e ervas daninhas é grande, incluindo-se um crescente número de neófitas.

A grande diversidade de espécies verificada é relacionada à grande diversidade de habitats, à fertilidade dos sedimentos e da água, à previsibilidade do pulso de inundação e à redução da competição interespecífica decorrente da redução anual das populações, provocada pelos ciclos de inundação e seca. Estes resultados corroboram o Conceito do Pulso de Inundação.

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