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A BIOSYSTEMATIC STUDY OF THE GENUS IMPERATA (GRAMINEAE: ANDROPOGONEAE)

Iowa State University PH.D. 1982

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A biosystematic study of the genus Imperata

(Gramineae: Andropogoneae)

by

Mark Lauren Gabel

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INTRODUCTION

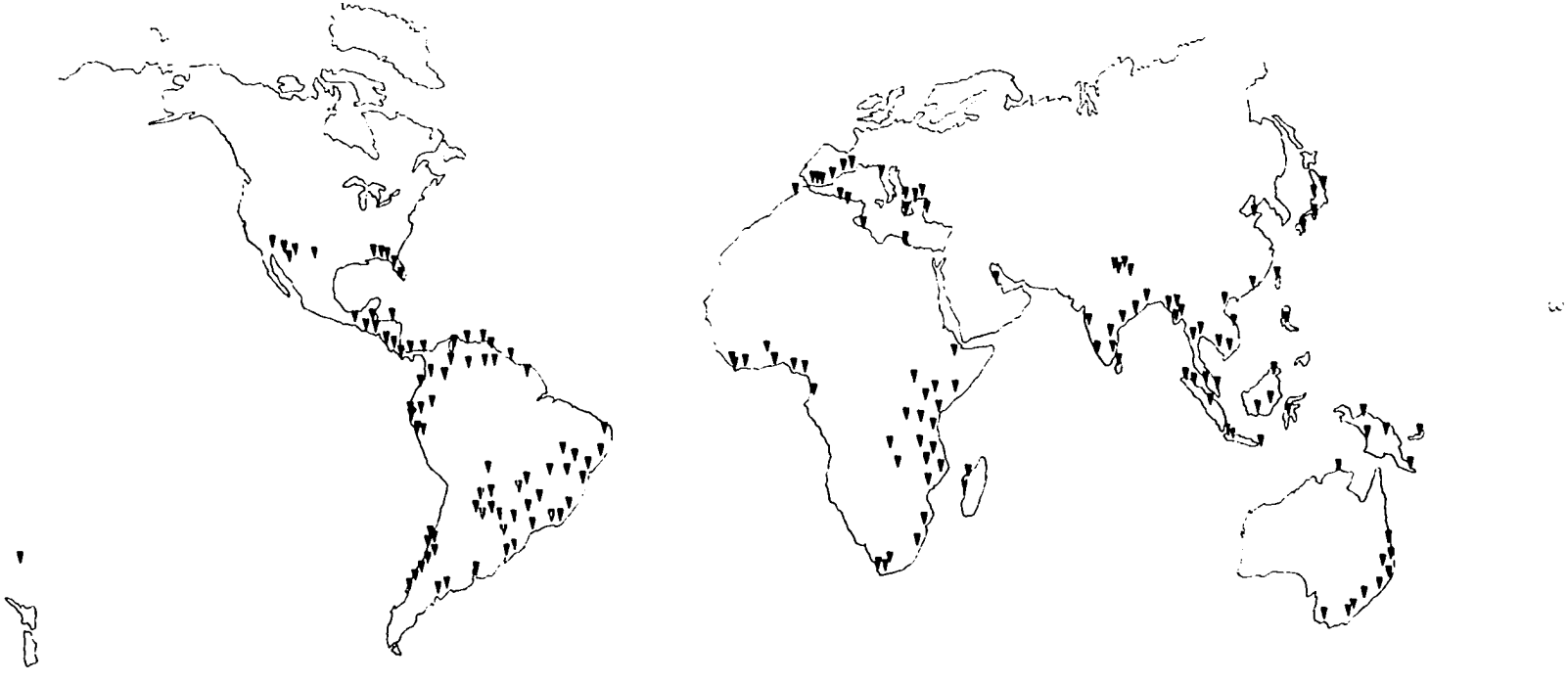
The genus Imperata is a member of the tribe Andropogoneae (Panicoideae). Distribution of Imperata is nearly worldwide in the warm regions of both hemispheres (Figure 1). The genus is important economically mainly because of the weedy characteristics of I. cylindrica. Holm (1969) and Holm et al. (1977) classified this species as one of the 10 worst weeds in the world. I. cylindrica has long been a problem in the Old World (Danhof, 1940; Vayssier, 1957; Eussen, 1978). The problem has been accentuated by slash and burn agriculture throughout the tropics, and military defoliation which has converted much forest in Southeast Asia to Imperata grassland (Westing, 1971). Imperata brasiliensis is also a weed in portions of South America (Aronovich et al., 1973).

Imperata serves as a host for fungi, bacteria, and insects which are pests of sugarcane, rice, and other economically important crops. In some cases, new shoots of Imperata are usable for hay or grazing. The hay has been used as thatching material, as a source of pulp for papermaking, or as a soil binder. In most instances, other plants have proven more productive or useful.

The taxonomy of the genus has been unstudied for nearly a century. The most recent work dealing with the genus as a whole was published by Hackel (1889) who described six species and six varieties.

The purpose of this study is to examine and evaluate the genus on a worldwide basis, delimiting the taxa by the use of morphological, anatomical, enzymatic, cytological, and distributional studies.

Figure 1. Distribution of Imperata. Triangles indicate collection sites of specimens used in numerical analysis



IMPERATA

THE POSITION OF *IMPERATA* WITHIN THE TRIBE ANDROPOGONEAE

The Andropogoneae are characterized by paired spikelets which are generally two-flowered, the lowest floret often being only staminate or barren. The elongated glumes remain attached to the florets upon disarticulation. On the whole, the tribe itself is quite well-defined, but at subtribal level has been split up into less defined groups.

Hackel (1889) described the Dimerieae, Sacchareae, Ischaemeae, Rotboellieae, and Euandropogoneae. Pilger (1954) split the tribe into six subtribes: Dimeriinae, Saccharinae, Ischaeminae, Rottboellinae, Soriginae, and Adropogoninae.

Clayton (1969, 1972) also has discussed the tribe. In his more recent work, he has enumerated seven subtribes, the Dimeriinae, Saccharinae, Germainiinae, Arthraxoninae, Andropogoninae, Anthistiriinae, and Ischaeminae. The Saccharinae were divided into two subgroups which are "a useful aid to taxonomic discussion, but are otherwise not of much importance." The Eulaliastrae is composed of *Eulalia*, *Homozeugos*, *Eulaliopsis*, *Polytrias*, *Apocopis*, *Pogonatherum*, *Lophopogon*, *Microstegium*, and *Ishnochloa*. The Saccharastrae contains *Eccoilopus*, *Imperata*, *Miscanthus*, *Miscanthidium*, *Sclerostachya*, *Spodiopogon*, *Eriochrysis*, *Saccharum*, *Erianthus*, and *Narenga*. The distribution of this group is mainly tropical and principally Asian. Clayton (1972) demonstrated the cohesiveness of this group with several numerical techniques.

In contrast, Hilu and Wright (1982) used cluster analysis in an attempt to study the Gramineae. In this study, the genera of the Andropogoneae were mostly clustered together, but within the tribe the classification did not resemble any traditionally accepted systematic schemes. The Saccharastrae were spread over the length of the tribe. The representation of the Andropogoneae proposed by Hilu and Wright (1982) seems unsatisfactory in light of other recent work.

MATERIALS AND METHODS

Herbarium Studies

Herbarium specimens were examined to determine distribution, ecological observations reported by collectors, local names, and morphological variation. Plants studied were from the following herbaria:

ARIZ -- University of Arizona Herbarium, Tucson

ASU -- Arizona State University, Tempe

AUA -- Auburn University Herbarium, Auburn, Alabama

BM -- British Museum (Natural History), London, England

BRY -- Brigham Young University, Provo, Utah

CR -- Herbario Nacional, Museo Nacional de Costa Rica, San José

EAP -- Escuela Agricola Panamericana, El Zamorano, Honduras

ENCB -- Escuela Nacional de Ciencias Biológicas, Instituto Polytécnico Nacional, México, D.F.

F -- Field Museum, Chicago, Illinois

FLAS -- University of Florida, Gainesville

ISC -- Iowa State University, Ames

ITIC -- Universidad Nacional de El Salvador, San Salvador

K -- Royal Botanic Gardens, Kew, England

LINN -- Linnean Society, London, England

LSU -- Louisiana State University, Baton Rouge

MEXU -- Universidad Nacional Autónoma de México, México, D.F.

MISS -- University of Mississippi, University

MO -- Missouri Botanical Garden, St. Louis

MNA -- Museum of Northern Arizona, Flagstaff

NMC -- New Mexico State University, Las Cruces

RSA -- Rancho Santa Ana Botanic Garden, Claremont, California

TAES -- Texas A&M University, College Station

TEFH -- Universidad Nacional Autónoma de Honduras, Tegucigalpa

US -- Smithsonian Institution, Washington, D.C.

USF -- University of South Florida, Tampa

VEN -- Instituto Botánico, Caracas, Venezuela

Herbarium codes are cited according to Holmgren et al. (1981).

Field Studies

I have been able to study Imperata in the field in the United States and Central America. Herbarium specimens were prepared and young inflorescences for determination of chromosome numbers were collected whenever possible. In several areas, numerous specimens were collected from single populations to determine within-population variability. Living rhizomes were collected to establish greenhouse populations.

Greenhouse Studies

Living material of Imperata rhizomes were transplanted to the greenhouse from the following countries: Argentina, Australia, Colombia, Costa Rica, Egypt, Honduras, Hong Kong, Indonesia, Japan, Mauritius, Peoples Republic of China, Republic of South Africa, Taiwan, Thailand, United States, and Venezuela.

Plants were grown in sand, kitty litter (Pohl, 1977), and potting soil. Light was provided by sunlight, incandescent lamps, high intensity sodium lights, and fluorescent lamps. Day length ranged from 9 to 16 hours, with most plants receiving 11 to 13 hour lengths. One group of plants was given a cold treatment (5° C) during the dark hours. Plants were clipped, burned with a propane torch, and subjected to crowding, freezing, and drought. Materials were periodically harvested for determination of chromosome numbers and for electrophoresis.

Morphological and Numerical Studies

Approximately 3,000 herbarium specimens of Imperata were examined using a dissecting microscope equipped with an ocular micrometer. Of these, 206 were selected for analysis based upon completeness of specimen and collection locality. Effort was made to insure that all regions of distribution were represented. Data were recorded for 22 variables as follows:

1) Culm length
2) Inflorescence length
3) Leaf width
4) Length of trichomes at blade base
5) Ligule length
6) Glume trichome length
7) Glume 1 length
8) Glume 2 length
9) Sterile lemma length

10) Sterile lemma width

11) Fertile lemma length

12) Fertile lemma width

13) Palea length

14) Palea width

15) Stamen number

16) Anther length

17) Stigma length

18) Style length

19) Ovary width

20) Ovary length

21) Lower inflorescence branch length

22) Distribution of trichomes on or near auricle

The large amount of data generated by these measurements was analyzed with the aid of a computer. Means, standard deviations, and ranges were calculated. Principal component analysis and cluster analysis were also used for data evaluation.

Principal component analysis is a type of ordination which uses variable scores to choose axes in multidimensional space. A detailed explanation is found in Morrison (1967). The procedure is similar to regression, but data are standardized (axes will then have the same units). The axes can then be rotated in space to find the "best fit." The line along which the data have a maximum spread is called the first principal component (or eigen vector, or latent vector). The axis at right angles

to this is the second principal component. The variances of the coordinates for each principal component are known as eigen values (or latent roots).

Thus calculation of principal components can be summarized in the three following steps:

1) Standardization of data using the formula

$$z = \frac{x - \bar{x}}{V}$$

where: z = the standardized score,
x = a value,
$\bar{x}$ = the mean of all x values, and
V = the variance of all x's.

2) The direction of the principal components is determined

3) New scores are calculated (the axes are rotated).

Eigen values and vectors were calculated for principal component analysis by using a SAS program (Barr et al., 1979).

Another method of analysis is clustering. This was done using the 206 operational taxonomic units (OTUs) and the variables listed in the Materials and Methods. The clustering procedure was done on standardized data. A correlation matrix was created by using the formula:

$$r = \frac{\Sigma\ (x-\bar{x})\ (y-\bar{y})}{\sqrt{\Sigma\ (x-\bar{x})^2\ \Sigma\ (y-\bar{y})^2}}$$

where: x = standardized x,
y = standardized y,
$\bar{x}$ = mean of standardized x,
$\bar{y}$ = mean of standardized y, and
r = correlation between x and y.

This process created a 206 x 206 matrix. The matrix was then transformed to facilitate the selection of OTUs with the highest correlations. The cluster program employed used the unweighted pair group mean method (Sneath and Sokal, 1973). Centroid linkage (rather than single or complete linkage) was used.

The two most similar OTUs were selected. The entire matrix was then recalculated using the centroid of the pair as a single unit. The next most closely correlated pair was then selected. The process was repeated until all OTUs were matched.

Anatomical Studies

Leaf blade clearings were made following the technique of Shobe and Lersten (1967). Cross sections of the leaf blades were made of both living and herbarium specimens. Leaf material for study was taken from the midpoint of the leaf blades. Herbarium material was first soaked overnight in Contrad 70 (Schmid and Turner, 1977). Then, all specimens were treated with 3.5% formaldehyde, 1% gluteraldehyde, and 0.05% phosphate buffer (pH 7). The specimens were then embedded in resin. The 1 μm sections were stained with toluidine blue in 1% sodium borate.

The scanning electron microscope was used to study external anatomy of spikelets and leaf blades. Material from live plants was used whenever possible. Samples were dissected in a buffered solution. Fixation in glutaraldehyde followed by OsO_4 and an EtOH dehydration series preceded a Freon series and critical point drying using CO_2. Some herbarium specimens were used. These were soaked in Contrad 70 for 12 hours at 60° C prior to their introduction to the EtOH-Freon series. Specimens were mounted on brass discs with silver cement and coated with Au-Pd in a Polaron E5100 sputter coater, then viewed at 15-25 kV in a JEOL JSM-35 scanning electron microscope. Photographs were taken using Polaroid type 665 positive-negative film.

Specimens of Imperata plus the following species of closely related genera were observed:

Erianthus compactus Nash
E. fulvus Nees ex Steud.
E. giganteus (Walt.) Muhl.
E. ravennae (L.) Beauv.
E. saccharoides Michx.
E. strictus Baldw.
E. alopecuroides (L.) Ell.
E. brevibarbis Michx.
E. contortus Baldw. ex Ell.

Miscanthus sacchariflorus Maxim. Hack.
M. sinensis Anderss.
M. floridulus (Labill.) Warb.
Saccharum officinarum L.
S. ciliare Anderss.
S. bengalense Retz.
S. spontaneum L.
Eriochrysis cayenensis Beauv.
E. holcoides (Nees) Kuhlm.

Chromosome Studies

Meiotic material for chromosome studies was obtained from wild plants and from the greenhouse. Newcomer's (1953) solution was used to preserve young inflorescences. Anthers were dissected out, squashed, and stained with propiocarmine (Sharma and Sharma, 1965).

Root tips were used to determine mitotic chromosome numbers. Techniques used were adapted from Palmer and Heer (1973). Pectinase in glycerol was substituted for aqueous pectinase. Exposure time to the pectinase was increased from one to three hours. Slides were made permanent by a freezing technique (Bowen, 1956). Drawings were made with the aid of a Zeiss drawing apparatus.

Electrophoretic Studies

Vegetative shoots of Imperata were harvested from greenhouse-grown plants when they were 5-10 cm tall and ground in liquid nitrogen and a crushing buffer (Mitton et al., 1979). The crushed shoots were then frozen at -40° C for later use. They were prepared for electrophoretic

analysis by allowing the frozen samples to thaw, and absorbing the liquid with wicks of filter paper. The paper was inserted in a horizontal starch gel. The gels were prepared using 12% Sigma electrostarch (lot 120F-0093). Sponge wicks were used to carry the current. Gels were run for two to five hours at 40 mA until the front had traveled 5 cm. Gels were sliced into three layers and stained for different enzymes using the recipes of Schall and Anderson (1974) and Shaw and Prasad (1970).

ANATOMY

Leaf blades of Imperata cylindrica have been studied by Duval-Jouve (1875), Pee-Laby (1898), Kirchner et al. (1904), Vickery (1935), Greiss (1957), and Metcalfe (1960). Falcão (1971) observed I. brasiliensis.

The most comprehensive study was authored by Greiss (1957). He studied vegetative portions of I. cylindrica in an attempt to identify plant materials from Egyptian tombs.

Metcalfe (1960) described the abaxial epidermis and a cross section of the lamina of I. cylindrica. He indicated the bicellular microhairs he observed had a pointed apex. I saw only rounded apices in specimens I observed, but collapsed hairs often appeared slightly pointed. Metcalfe also indicated triangular subsidiary cells were common.

I studied cross sections of Imperata leaf blades (Figures 2-7). The most prominent features of the cross sections are large vascular bundles which alternate with smaller bundles. Bulliform cells occur above the smaller bundles. Pee-Laby (1898) reported bulliform cells were not well-developed in Imperata. Major vascular bundles were surrounded by a double bundle sheath, which supports the finding of Downton (1975) that Imperata species have C_4 photosynthesis.

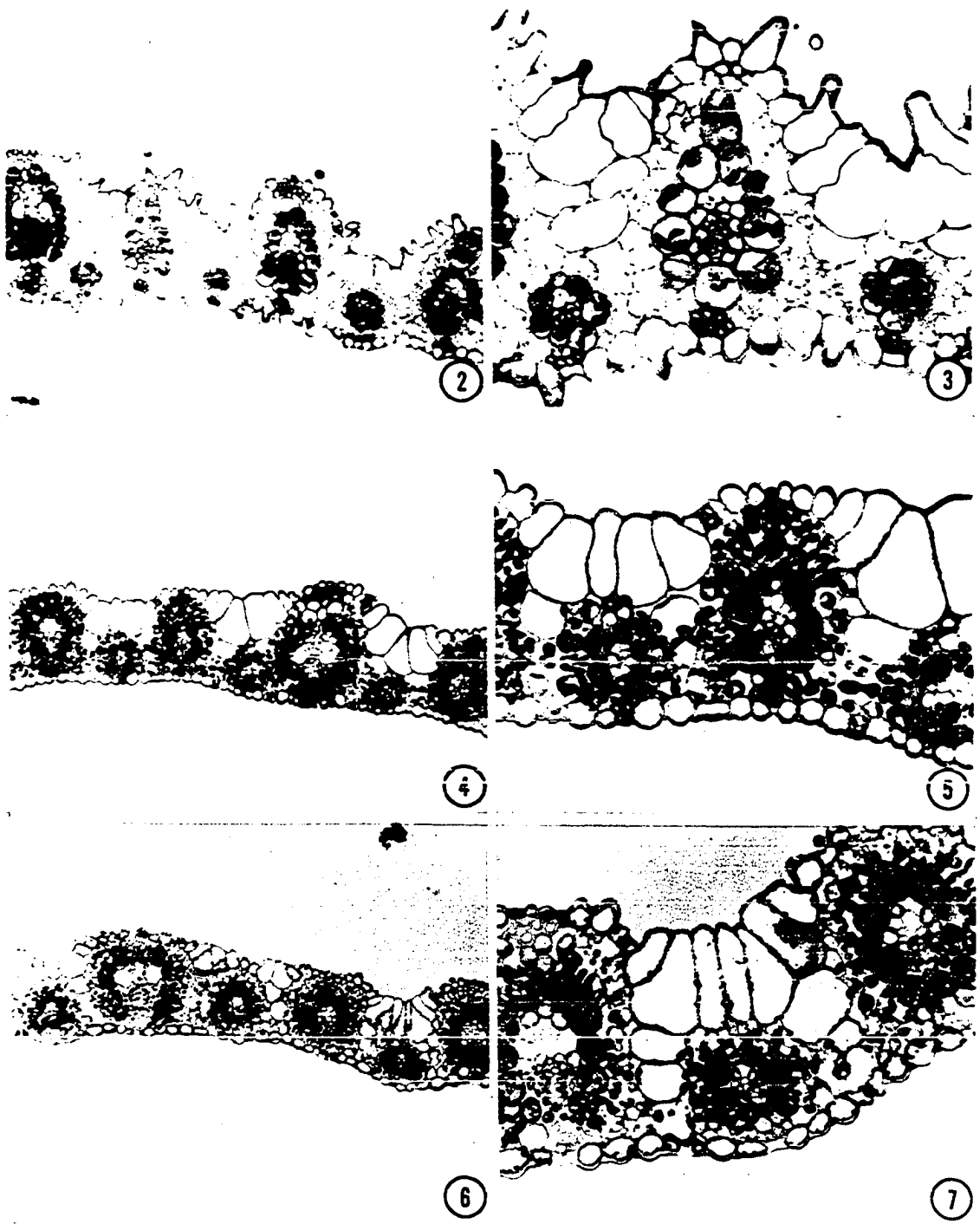
The midrib of the leaf blade appears white macroscopically. Internally, the midrib contains many parenchyma cells and a number of vascular bundles of various sizes. Toward the base of the blade the

Figures 2-7. Cross sections of *Imperata* leaf blades. Left column 145x, right column 346x

Figures 2 and 3. *I. minutiflora* (herbarium material US 1536571, Venturi 811, Argentina)

Figures 4 and 5. *I. brevifolia* (live material of Gabel 1979, Arizona, USA)

Figures 6 and 7. *I. cylindrica* (live material of RSA South Africa)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lamina is greatly reduced and the midrib is predominant, with many vascular bundles. Duval-Jouve (1875) pointed out that there is structural variation between the apex and base of the leaf, including an increased number of vascular bundles.

The great number of large papillae on the epidermal surfaces of I. minutiflora was the major observable specific difference in cross sections of leaf blades.

Figures 8-11 show the variation between the abaxial and adaxial epidermis. The adaxial surface is covered with papillae and epicuticular wax. Papillate subsidiary cells as described by Palmer and Tucker (1981) are distinctive (Figure 11). Of the related genera surveyed for epidermal characters (see Materials and Methods for a listing), no other groups had these well-developed papillate subsidiary cells (Figures 12-15). This character is known in other groups of the grass family. Palmer and Tucker (1981) reported papillate subsidiary cells in all surveyed members of the Oryzeae.

The abaxial surface of all Imperata specimens surveyed is relatively smooth in comparison to the adaxial surface and has much less epicuticular wax. The subsidiary cells of the lower surface are also less developed and may appear triangular in clearings as reported by Metcalfe (1960).

Hackel (1889) noted that the culms of I. exaltata were hollow, while culms of other species were solid. I sectioned over 100 culms of various taxa and found solid internodes present in young culms, and hollow internodes in older plants. This character, like most anatomical

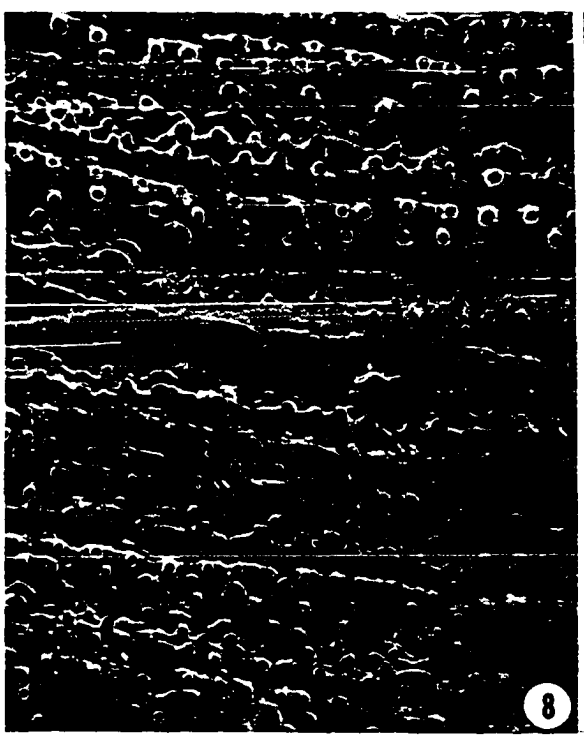
Figures 8-11. Scanning electron micrographs of the epidermis of *Imperata cylindrica* (Gabel 1942)

Figure 8. Adaxial epidermis, 240X

Figure 9. Stoma showing papillate subsidiary cells and epicuticular wax, 2600X

Figure 10. Abaxial epidermis with stoma, 2000 X

Figure 11. Stoma on abaxial epidermis, 3600 X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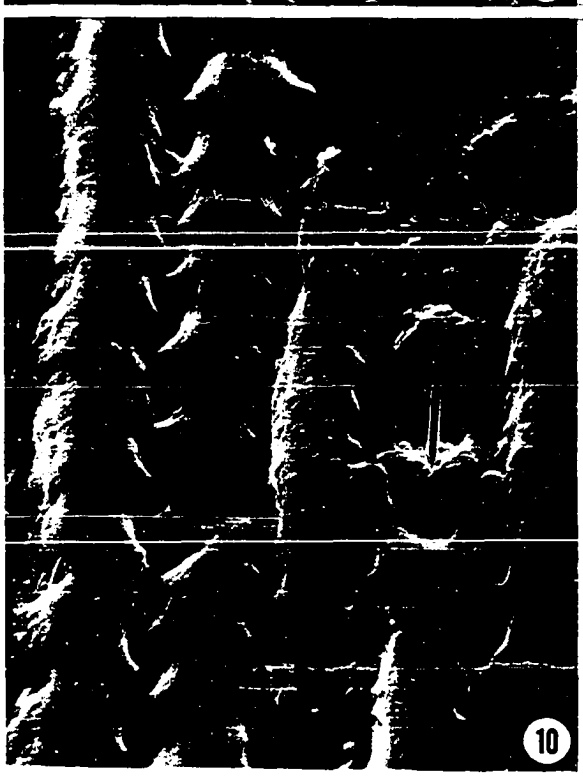
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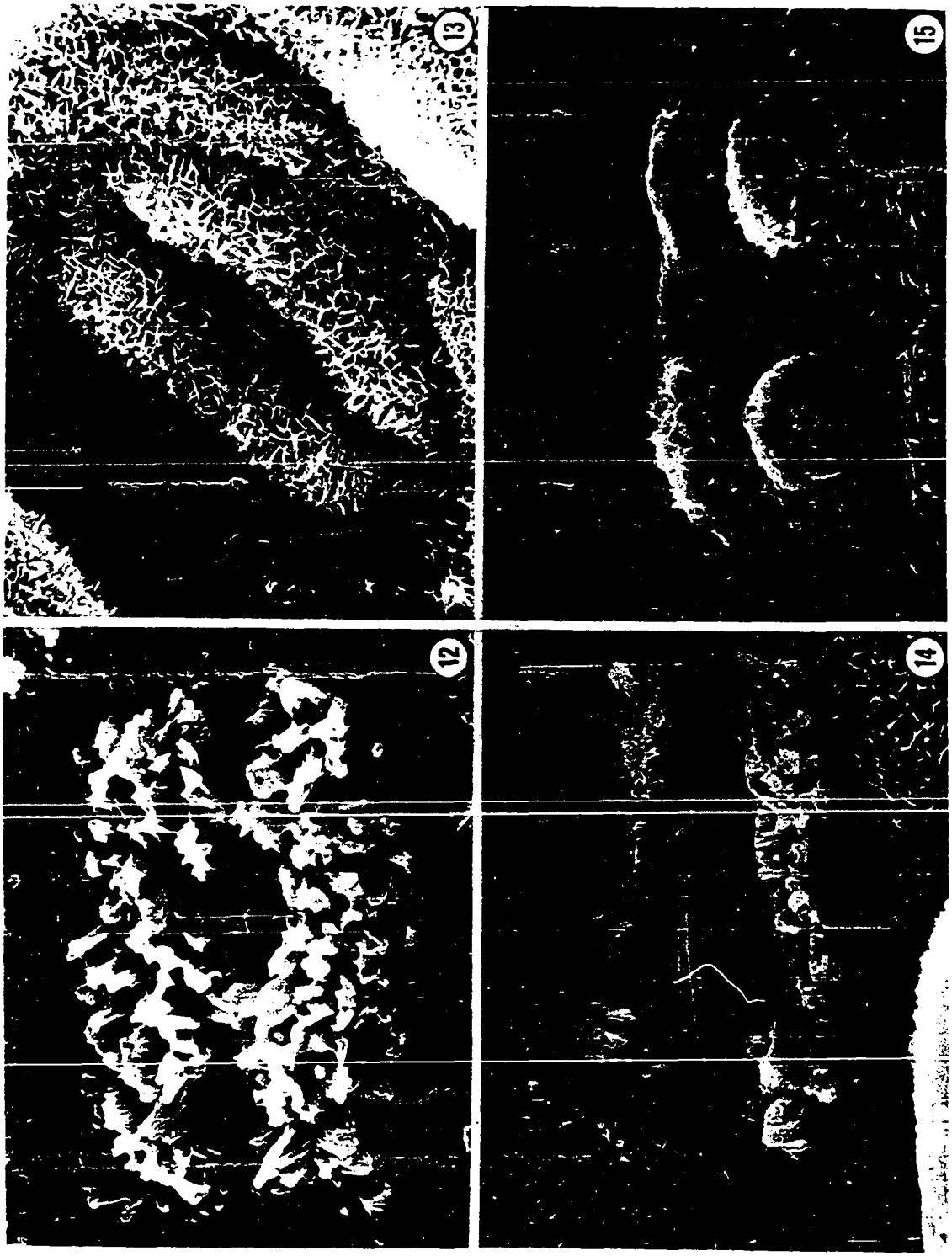
Figures 12-15. A comparison of adaxial stomates in *Imperata* and related genera

Figure 12. *Miscanthus sinensis* (Britt 3054, N. Carolina), 4000X

Figure 13. *Eriochrysis cayanensis* (Pohl and Davidse 12047, Honduras), 2600X

Figure 14. *Erianthus alopecuroides* (Godfrey 72831, Florida), 3200X

Figure 15. *Imperata cylindrica* (Gabel 1898, Mississippi), 3000X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characters surveyed, did not prove to be a good indicator of specific differences.

CHROMOSOME NUMBERS

Base chromosome numbers in the Andropogoneae are x = 5, 9, and 10 (Gould, 1968). *Imperata* chromosome numbers are included in Table 1.

Table 1. Previously reported chromosome numbers in species of *Imperata* (reported or calculated somatic number)

Taxon	Chromosome Number	Authority
I. cylindrica	20	Bremer, 1925
	20	Janaki-Ammal, 1941
	20	Tateoka, 1953
	20	Roux and Adjanohoun, 1958
	20	Chen and Hsu, 1962
	20	Mehra et al., 1962
	20	Larsen, 1963
	20	Singh, 1964
	20	Tateoka (in Löve, 1967)
var. *europea*	40	Roux and Adjanohoun, 1958
var. *africana*	c. 60	Roux and Adjanohoun, 1958
	60	Tateoka, 1965
	60	Harvey (in Löve, 1966)
	60	Fernandes and Queiros, 1969
I. conferta	20	Price and Daniels, 1968
	20	Reeder and Soderstrom (in Löve, 1968)
I. contracta	20	Pohl and Davidse, 1971
	20	Davidse and Pohl, 1974

Roux and Adjanohoun (1958) reported chromosome numbers of 2n = 40 and about 60 in specimens from France and the Ivory Coast, respectively. These were correlated with Hubbard's (1944) varieties (europea and africana). The Asian chromosome reports of 2n = 20 are representative of Hubbard's variety major.

In this study, chromosome numbers were determined for specimens from Honduras, Indonesia, Thailand, Australia, and the United States (Figures 16-24 and Table 2). Voucher specimens are deposited at ISC.

Table 2. Chromosome numbers determined in this study from Imperata species

Proposed Taxon	Somatic	Gametic	Material
I. cylindrica	--	10	Gabel 1912 (Florida)
	20	--	YSN 3 (Thailand)
		10	INDO (Indonesia)
	20	--	AUST (Australia)
I. brevifolia	--	10	Gabel 1979 (Arizona)
	--	10	Gabel 1980 (Arizona)
I. contracta	20	10	Pohl and Gabel 13711 (Costa Rica)
	20	--	Pohl and Gabel PROG (Honduras)

First counts for I. brevifolia are n = 10. This species, like others in the genus, has 10 gametic or 20 somatic chromosomes. Chromosome numbers for several proposed taxa are not available because of lack of cytological material.

Figures 16-24. Chromosomes of Imperata, scale = 10 μm

Figure 16. I. cylindrica n = 10, Gabel 1912

Figure 17. I. cylindrica 2n = 20, YSN

Figure 18. I. cylindrica 2n = 10, INDO

Figure 19. I. cylindrica 2n = 20, AUST

Figure 20. I. brevifolia n = 10, Gabel 1979

Figure 21. I. brevifolia n = 10, Gabel 1980

Figure 22. I. contracta 2n = 20, Pohl and Gabel PROG

Figure 23. I. contracta n = 10, Pohl and Gabel PROG

Figure 24. I. contracta 2n = 20, Pohl and Gabel 13711

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REPRODUCTIVE BIOLOGY

Soerjani and Soemarwoto (1969) have studied rhizomes of Imperata cylindrica. They found that sprouting of buds is optimal at 30° C, and that whitish-colored buds sprouted more readily than brown buds. Soerjani (1970) found that fragmenting rhizomes "will break the apical dominance" allowing rhizome buds to sprout. A high percentage of two-noded rhizome fragments were reported to grow. One-noded rhizome fragments were observed sprouting only when buds were visible.

Tripathi and Harper (1973) compared the reproductive biology of Agropyron caninum and A. repens. Both reproduce by seed and by tillering. A. repens also reproduces by rhizomes. A. repens was shown to have 45-55% subterranean biomass, while A. caninum had 14-16%. Several taxa of Imperata I tested proved to have 33-49% subterranean biomass.

Variability in plant populations which reproduce vegetatively is said by Grant (1971) to be less than those populations which exhibit agamospermy or sexual reproduction. Silander (1979), in a study of Spartina patens, found that population variability patterns were dependent upon habitat stability. Plants in a harsh environment were shown to have low diversity, while populations in more favorable environments were shown to have higher diversity. A great deal of morphological diversity has been observed in Imperata, which may correlate with its wide geographical distribution.

In addition to vegetative reproduction, the Imperata are capable of sexual reproduction. A great diversity of flowering regimes has been exhibited. Santiago (1965) observed in Malaya that some Imperata never flowered, some flowered frequently, and many were intermediate, some of these flowering only upon defoliation.

I have observed a similar situation in the southeastern United States. I made local inquiries as to the blooming frequency of many populations situated near residences. At one site, a home was completely surrounded by Imperata. The occupants of the residence indicated that they had occupied the home for 30 years and had not observed blooming at that site. They had noticed blooming at other sites. Other residents at other sites reported blooming annually, or less frequently. In most cases, the residents noticed the populations of Imperata were expanding. Paisooksantivantana (Dept. of Agriculture, Bangkok) reported fire-induced blooming of Imperata in Thailand. Eussen and Soerjani (1975) reported slash/burn treatments induced flowering, but florets were seldom fertile after such treatment. Ward et al. (1940) reported blooming in Florida following a freeze.

I was unable to induce flowering under greenhouse conditions. Burning, clipping, fertilizer, transplantation, change in day length, and cool nights (eight hours at 4° C) had little effect on the blooming of the plants (Table 3). Some of the replicates bloomed regardless of the treatment, while others could not be induced to bloom.

In plants grown in the Iowa State Botany greenhouse, anthers protruded from spikelets a day prior to the emergence of stigmas in the

Table 3. Blooming in greenhouse specimens of Imperata

Specimen	Treatment					
	Control	Clipped	Burned	Cool Nights	Transplant[a]	Hi P[b]
1895	X[c]					
1898						
1902						
1906						
1896						
1897						
1907						
1905					X	
1910						
1912						
1927						
1931						
1932						
1937						
1938						
1941						X
1943						
PROG	X	X	X		X	X
13711						
Indo2	X					
Indo5						
Indo6						
Indo9						
Indo11						
Indo14						
Indo15	X				X	
Indo16						
Colo						
Ti 3						

[a]Transplant = plants transplanted to large flats.

[b]Hi P = 0-46-0 fertilizer.

[c]X = blooming plant.

florets on the upper one-third of the inflorescence. The following day, two-thirds of the florets had visible anthers, while the stigmas on the top one-fourth of the inflorescence were observable. By the third day, all anthers were visible, but only half the stigmas were seen. Another two days passed before all stigmas were protruding. Several days after the initiation of anthesis the inflorescences became "fluffy" because of the spreading of the long trichomes attached to the callus.

Stamen number in Imperata is one or two, which is apparently reduced from three, the number common to most grasses.

Seeds appear to have no dormancy requirements. Santiago (1965) reported 95% germination within one week. He also reported that seeds remain viable for at least one year.

Mature caryopses are extremely small. Most I have measured are about 1 mm long. The long trichomes of the spikelet allow the caryopses to be carried on air currents. Ridley (1930) gave an average flight distance of 16 m from inflorescence level.

Santiago (1965) reported that gametes of I. cylindrica are self-compatible, but that the species was essentially outbreeding and seedlings from one inflorescence "were very variable in morphology."

I attempted to self-pollinate several inflorescences of PROG, INDO, and several southeastern U.S. populations. I was never successful. This evidence, plus the fact that in field collections of small isolated populations I have not observed seed set, leads me to speculate that some type of self-incompatibility mechanism may be present in at least some groups of Imperata. Additional evidence from observation of meiosis

indicates no irregularities which might disrupt normal sexual reproduction.

NUMERICAL STUDIES

I calculated the first three principal components for all 206 selected OTUs. I began a three-dimensional plot of all OTUs, but soon saw that it would be impossible to distinguish groups due to the large number of individuals. I decided to model the system using a 4 x 8 sheet of pegboard to represent the first two component axes. I used wooded dowels of various heights to represent the third components. From the model (Figure 25), it is possible to distinguish groups or clusters of OTUs. To facilitate recognition of these groups, a mean of each group was calculated and is represented in Figure 26. There appear to be nine groups. Group 1 was, by far, the largest in terms of number of OTUs included and likewise expressed the most diversity. Group 2 stood by itself at the opposite end of the model. Groups 3, 4, 5, and 7 formed the central section of the model. They were separated by the first and third components. Group 9 was allied with, but separated from Group 3.

The cluster analysis (Figure 27) was also indicative of relationships. Two major groups were immediately obvious. The group at the left was composed of plants with narrow inflorescences, mostly cylindrical throughout their length. The major group at the right was composed of plants which had a more conical inflorescence, the lower branches of the panicle being proportionately longer than those of the left group.

Figure 25. Principal component analysis model of Imperata

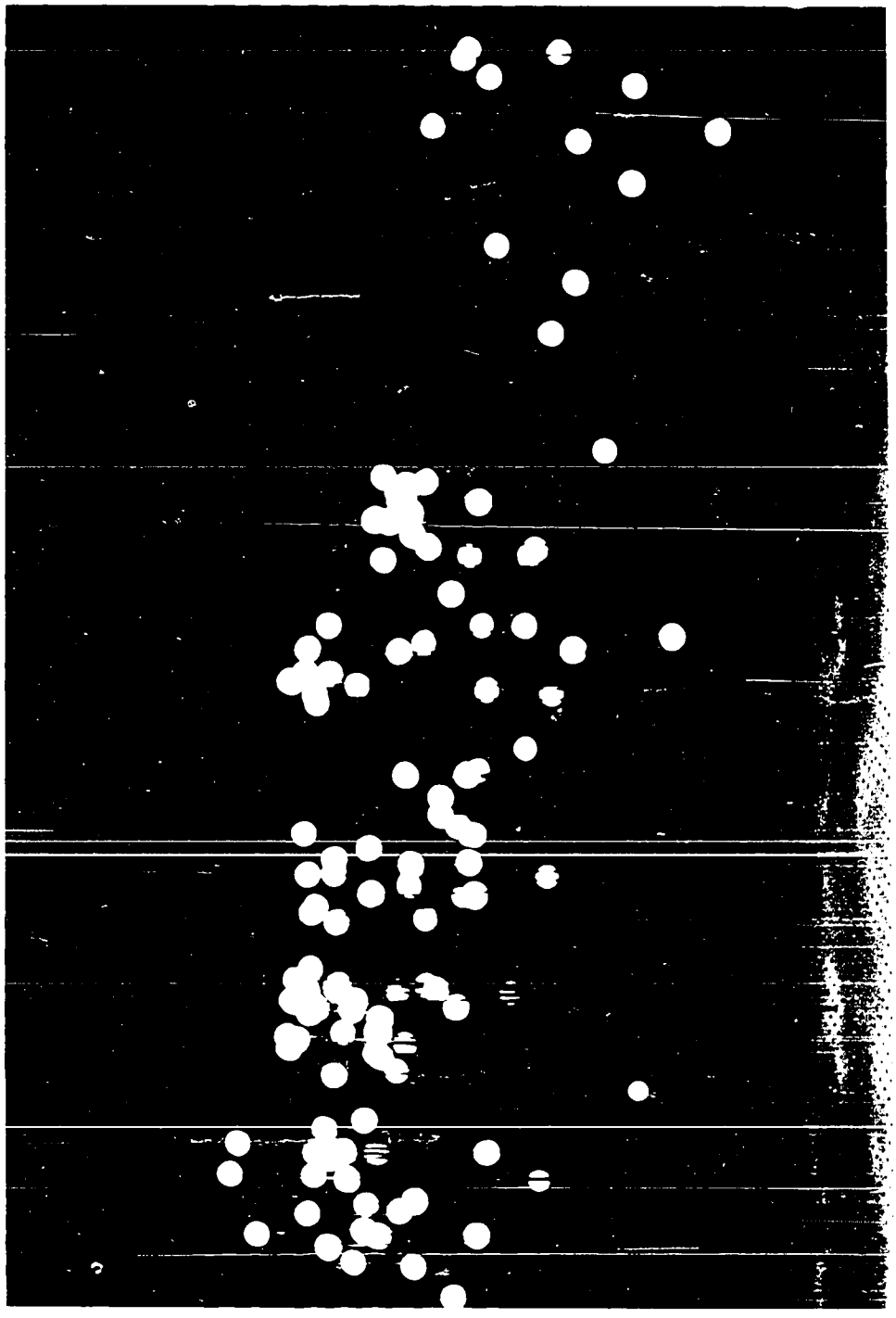


Figure 26. Means of clusters from principal component analysis. Roman numerals indicate first, second, and third principal components

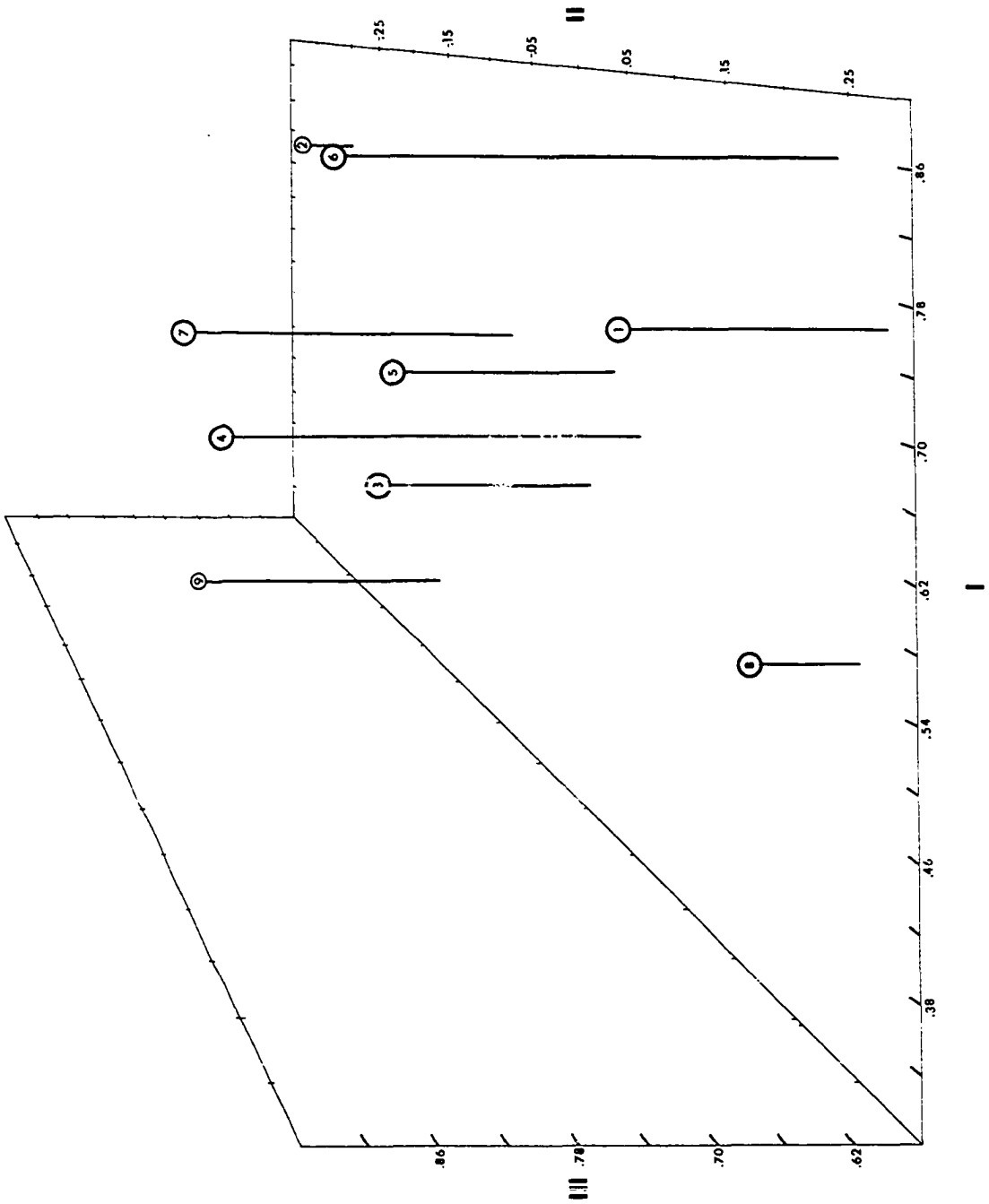
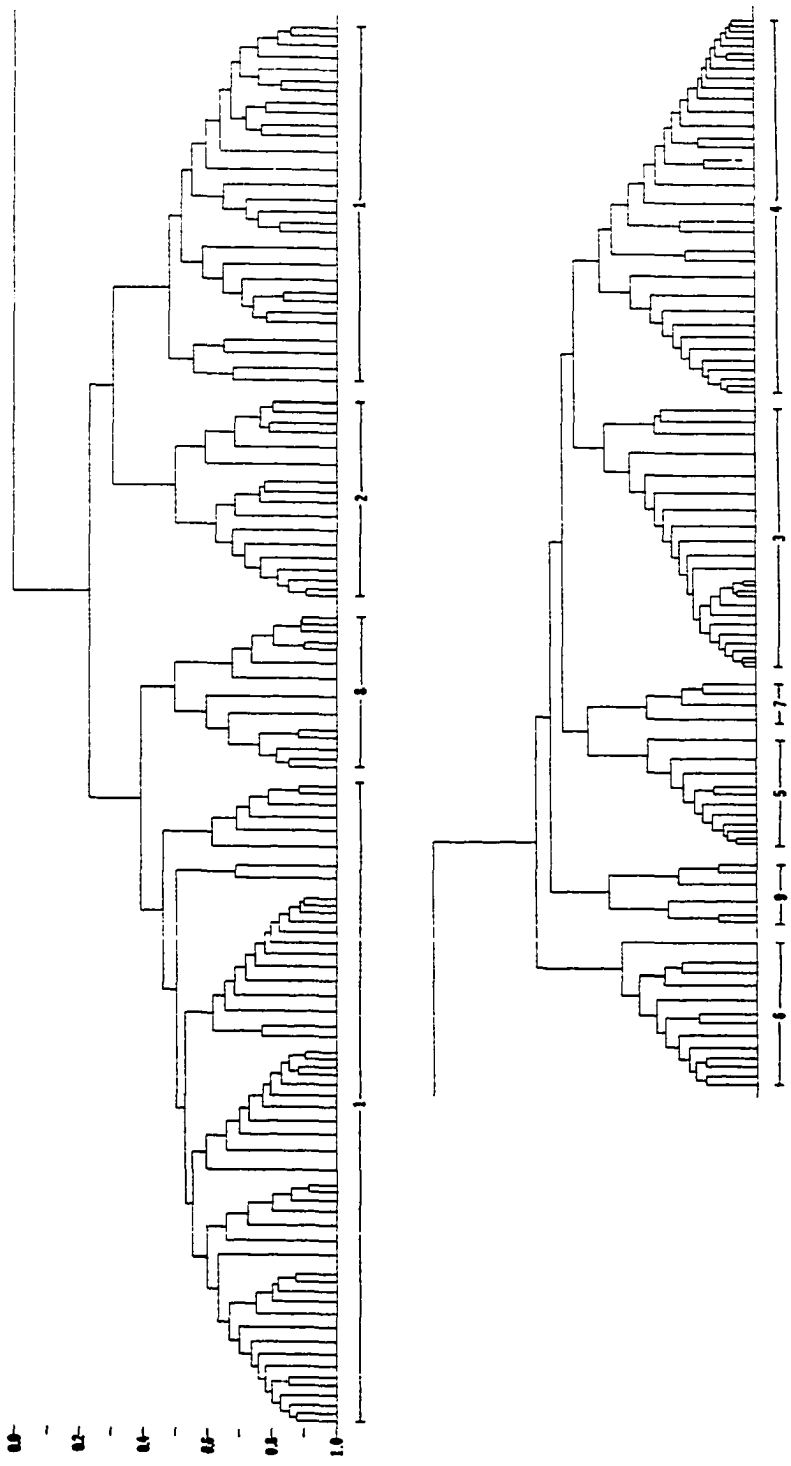

II
-.25
-.15
-.05
.05
.15
.25
.86
.78
.70
.62
.54
.46
.38
I
III
.86
.78
.70
.62
1
2
3
4
5
6
7
8
9

Figure 27. Dendrograph of 206 specimens of Imperata. Numbers on the y-axis represent correlation. Numbers on the x-axis represent principal component groups



A phenon line (Sneath and Sokal, 1973) has been constructed for the dendrograph (Figure 27). This line runs the length of the dendrograph and is an arbitrary boundary beyond which taxa or phenons may be chosen. This must be applied at the same level throughout the analysis. Sneath and Sokal (1973) do include a disclaimer in their definition of phenon, stating that they

> are groups that approach natural taxa more or less closely and, like the term taxon, can be of any hierarchic rank or of indeterminate rank. Since they are groups formed by numerical taxonomy, they are not fully synonymous with taxa; the term 'taxon' is retained for its proper function, to indicate any sort of taxonomic group.

By selection of a phenon line at 0.45 (on the correlation scale), nine groups are again represented. Beginning at the extreme left, I will discuss each group in turn, comparing it to the principal component analyses. Labels on the x-axis of the dendrograph are the labels of similar groups in the principal component analysis (PCA).

Group 1 (PCA) is split into two groups by the dendrograph. An analysis of the two indicates that the group on the left is from the Mediterranean and Africa, while the group on the right is from India and Asia. An examination of the data indicates that the major difference between the groups is spikelet size. The groups can be separated statistically, but the standard deviations and ranges overlap extensively.

Group 8 was restricted to plants occurring in Chile. Group 2 contained only South American plants.

Moving to the major cluster on the right, the first group delimited by the 0.45 phenon line is PCA Group 6. These plants are mainly from

Brazil, with a few from neighboring countries (Bolivia, Argentina, and Paraguay). Group 9 is composed of plants from the New Zealand area. Group 5 is composed of South American plants, mostly from Argentina, Peru, Ecuador and Bolivia. Group 7 has been partially submerged in Group 5 or dispersed to Group 4. The right branch of Group 5 is composed of a portion of Group 7 (PCA). Group 3 is composed of plants from Southeast Asia and the Pacific Islands, while Group 4 is chiefly plants from Central and South America.

A comparison of the numerical results with taxa reported by other workers would be in order.

Group 1 compares well to published descriptions of Imperata cylindrica. Hubbard (1944) split I. cylindrica into five varieties. The group on the extreme left of the dendrograph represents his varieties europea and africana. The cluster representing the second number 1 in the dendrograph is composed of plants that Hubbard would have referred to varieties major and latifolia. Group 8 corresponds to Hubbard's I. cylindrica var. condensata. This group was given specific status by Steudel in 1855, and is the only group of New World Imperata with two stamens. Both PCA and cluster analysis indicate the distinctness of this group.

Group 2 corresponds well to descriptions of I. brasiliensis. Plants in this group usually have reduced or lacking fertile lemmas. Inflorescences are generally shorter than those of other groups.

Group 6 is composed of South American plants. Most members of this group have narrow leaves and elongated ligules. This group corresponds to descriptions of I. tenuis.

Group 9 consists of plants found only in the region north of New Zealand known as the Kermadec Islands. These plants were easily distinguished from other groups of Imperata by the extremely short trichomes on the spikelets. The short trichomes reveal more of the glumes than are visible in other Imperata, thus giving the entire inflorescence a brown appearance. Hackel (1903) named these I. cheesemanii. The inflorescences are generally longer proportionally to the culms.

Group 7 is restricted to specimens collected from the southwestern United States and northern Mexico. The plants are characterized by long trichomes and elongated ligules. This is the least distinct group in the numerical analysis. This phenon represents I. brevifolia of Vasey (1886).

Group 3 corresponds to I. conferta of Ohwi (1941). These plants range from Southeast Asia through the Pacific Islands, and are most easily recognized by their long conical inflorescences.

Group 4, from Central and South America, fits the description of I. contracta given by Hitchcock (1893). They also have elongated basal inflorescence branches.

ELECTROPHORESIS

Electrophoresis has often been used as a taxonomic tool by animal systematists, but has only recently come into wide use by botanists. Gottlieb (1977) described the advantages and limitations of its use in plants. The differential electrophoretic mobility of enzymes is an indicator of the accumulated mutations in the gene specifying the enzyme. Enzymes are separable due to variation in electric charges resulting in differential migration through an electric field. Migration in the field may also be affected by molecular size or configuration. Specific histochemical staining reveals the location of the enzymes in the field (gel).

Different forms of an enzyme that catalyze the same reaction are called isozymes when produced by different loci. Allozymes are coded by different alleles of the same locus. These variants may be a result of substitutions, deletions, or additions of amino acids in the polypeptide. Such changes may or may not affect migration.

Shaw (1970) pointed out that only 30% of the substitutions of nucleotides will actually produce differences in the mobility of amino acids. Thus, electrophoretic evidence actually provides an underestimate of the genetic differences between taxa. Hamrick et al. (1979) found "no evidence to indicate that there is a bias in the detection of variability that is associated with any life-history or ecological variable."

The difference observed in mobility can be a result of one change or many. Gottlieb (1977) indicated that there is likely to be greater difference with greater phylogenetic distance.

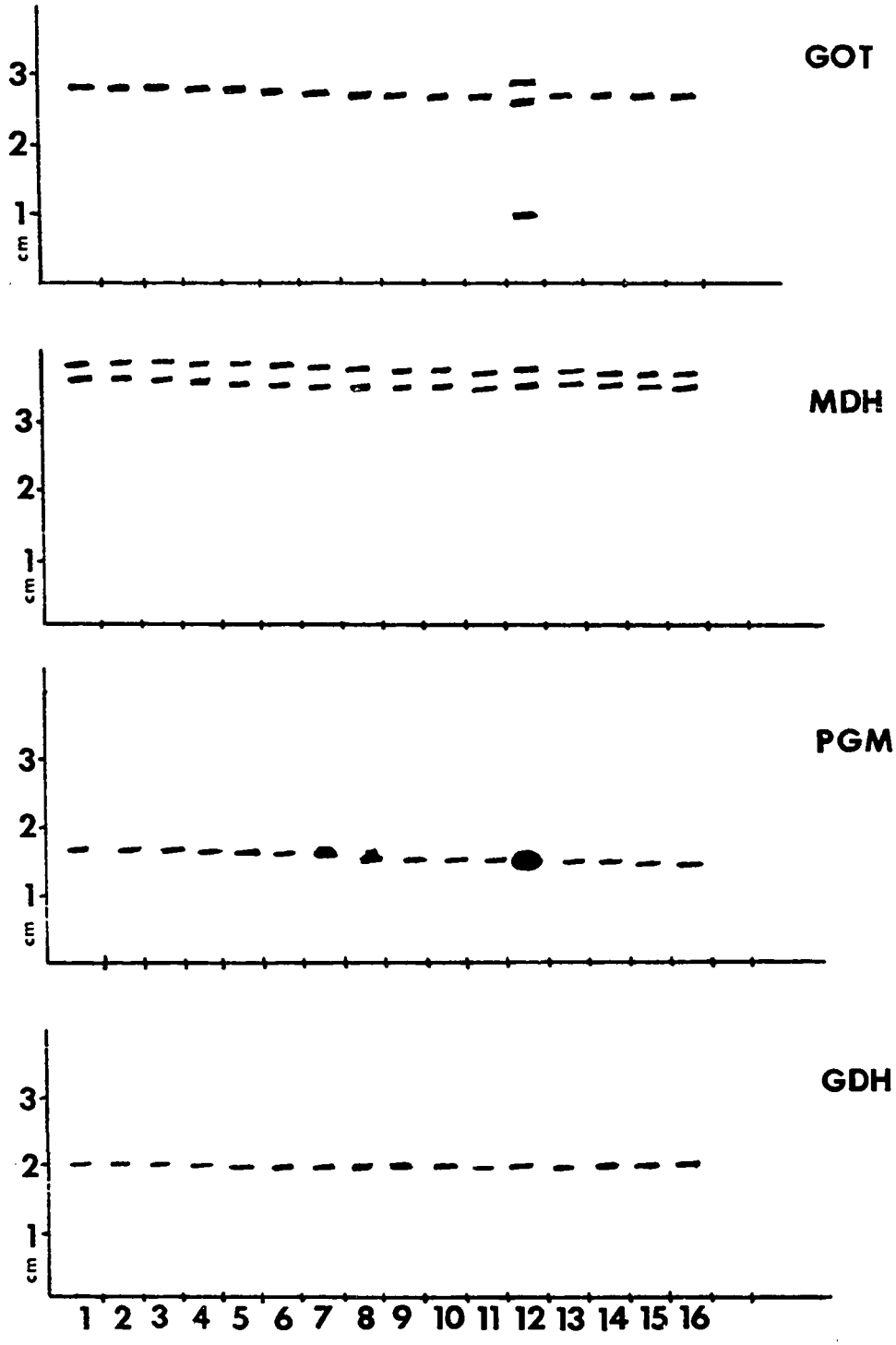
Fifteen individuals collected along a transect of population 1960 from Mississippi were electrophoresed with several gels and buffer systems. Figure 28 shows the results of staining for Glutamate-Oxaloacetate Transaminase (GOT), Malate Dehydrogenase (MDH), Phosphoglucomutase (PGM), and Glutamate Dehydrogenase (GDH). The same standard (Indo) was run with all individuals.

The results indicate that the population is probably composed of individuals which are very similar genetically. On the basis of the four stains, no variation was detectable. This similarity in banding patterns is correlated with a high degree of morphological similarity in the population. It seems likely that this population is a clone.

One population is a small representative of the actual diversity present in the species. Other individuals from the southeastern United States were also analyzed for GOT. This yielded a completely different result. Two individuals of population 1960 were compared with specimens from populations 1897, 1902, 1939, and 1943. Three of the populations (1960, 1902, 1898) probably have only one locus. These plants were collected in Mississippi. Populations 1939 and 1943 may have two loci, and were collected in Florida.

Stains for GDH, MDH, GOT, and EST (Esterase) were used to determine the presence of these enzymes on plants from Asia, Central America, South

Figure 28. Tracing of banding patterns of population 1960 on four different enzyme systems. Individual 12 (Indo 16) is a standard


GOT
MDH
PGM
GDH
3
2
1
cm
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16

America, Africa, and Australia (Figures 29 and 30). The GDH gels showed similar banding patterns in plants from Thailand, China, Indonesia, Australia, Mauritius, Egypt, and the Republic of South Africa. All three populations from Grand Canyon National Park in the Southwestern United States exhibited similar banding patterns. Enzymes from Honduran plants migrated more rapidly than any others observed. Banding patterns exhibited by plants from Colombia were similar to those from the Grand Canyon.

The same groupings were repeated with MDH, with the exception that the banding pattern indicated double bands for all but the Honduran plants. EST gels indicated that four plants from the southeastern United States were similar to plants from Central America (13711 and PROG). Plants from Indonesia all exhibited similar banding patterns. GOT demonstrated similarities between Asian Imperata and some representatives from the southeastern United States (1939 and 1943). Central American plants (13711 and PROG) showed similar bands, yet were different from the other groups.

These data indicate little variability in population 1960. It is possible to separate OTUs from taxa 1, 4, and 7 on the basis of differential migration patterns of EST, GOT, MDH, and GDH. Plants from the Grand Canyon exhibited banding patterns similar to those from Colombia. PROG (from Honduras) was placed in Group 4 with Colombian plants by the numerical analyses, yet showed different electrophoretic patterns.

Gottlieb (1977) warned against evaluation of electrophoretic analysis by "simply counting the number of bands with similar and dissimilar

Figure 29. Tracings of banding patterns of Imperata individuals stained for three enzymes. Labels for the first two gels (GDH and MDH) are the same. S indicates standard (Indo 16)

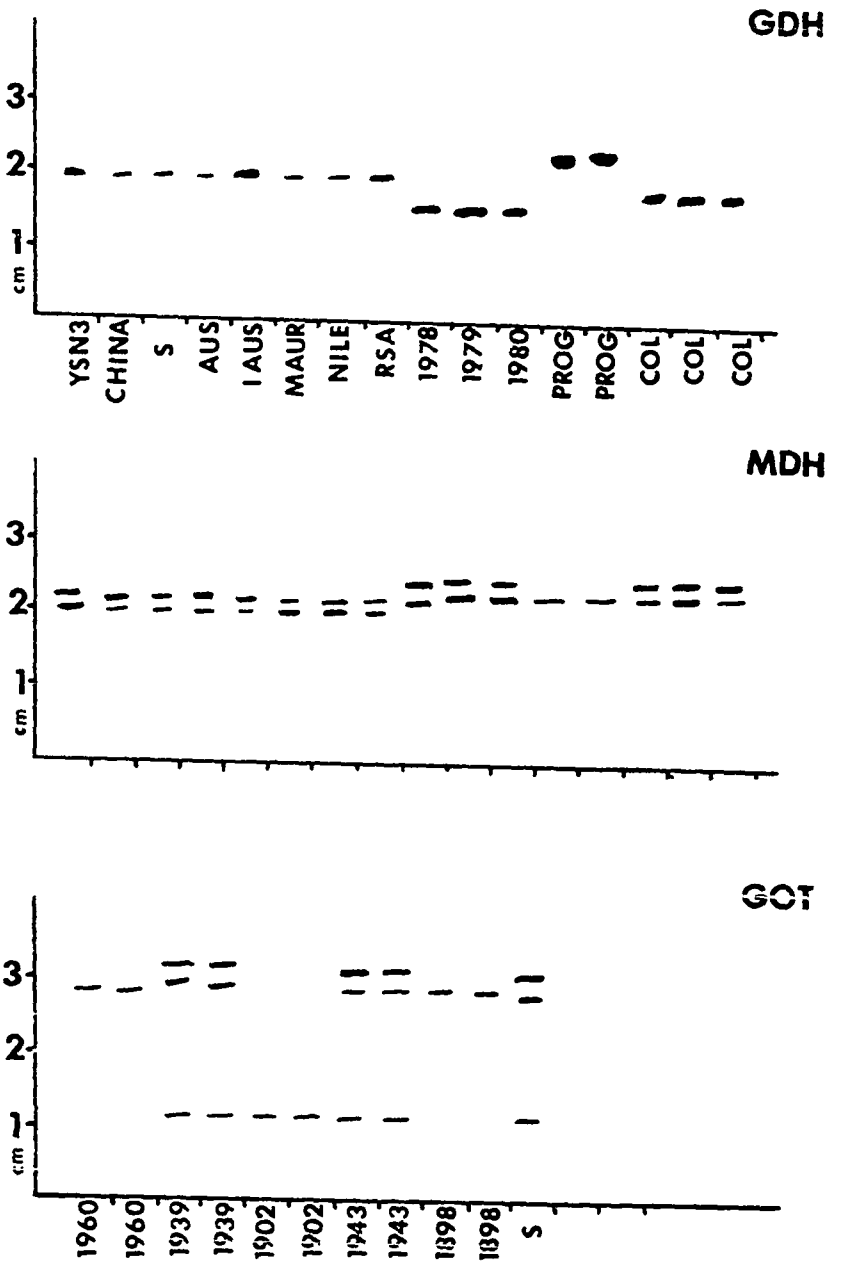
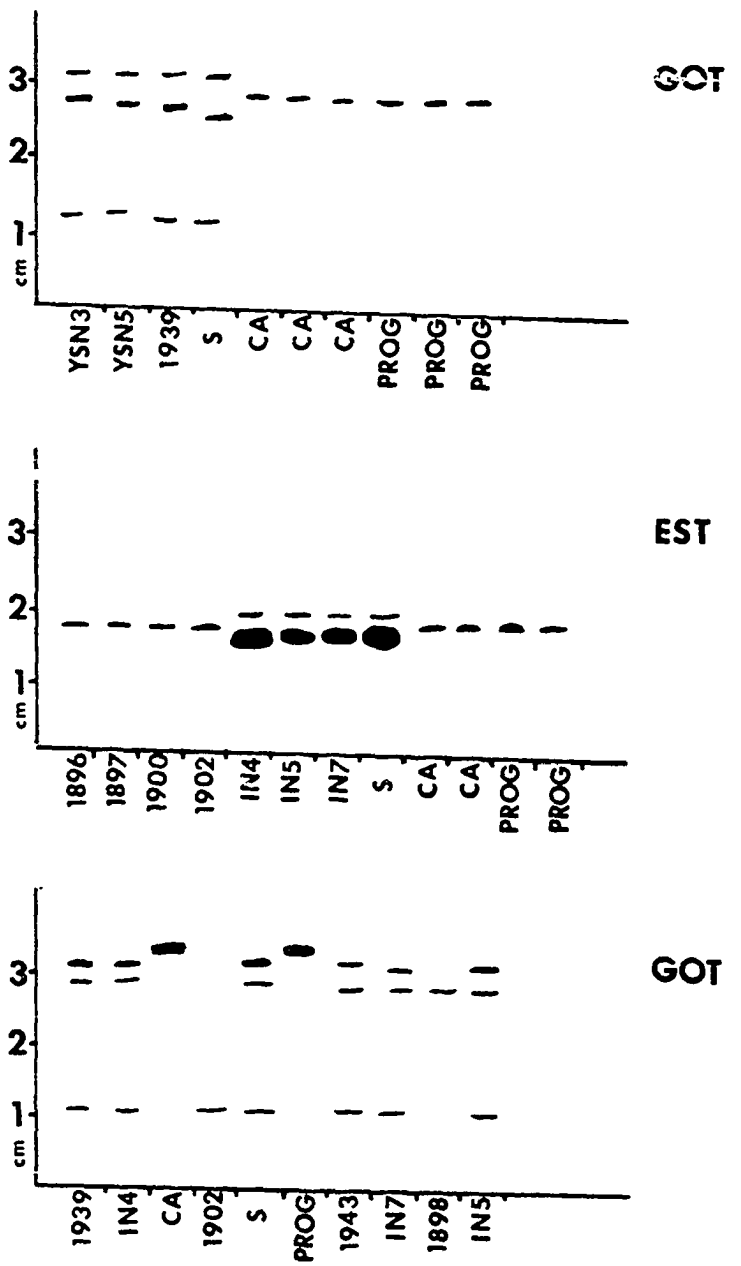

GDH
3
2
1
cm
YSN3
CHINA
S
AUS
I AUS
MAUR
NILE
RSA
1978
1979
1980
PROG
PROG
COL
COL
COL
MDH
3
2
1
cm
GOT
3
2
1
cm
1960
1960
1939
1939
1902
1902
1943
1943
1898
1898
S

Figure 30. Banding patterns exhibited by Imperata individuals on starch gels stained for GOT and EST. S is standard (Indo 16)


GOT
3
2
1
cm
YSN3
YSN5
1939
S
CA
CA
CA
PROG
PROG
PROG
EST
3
2
1
cm
1896
1897
1900
1902
IN4
IN5
IN7
S
CA
CA
PROG
PROG
GOT
3
2
1
cm
1939
IN4
CA
1902
S
PROG
1943
IN7
1898
IN5

mobilities." Unfortunately, not enough data have yet been collected for sound analysis of genetic distances (Nei, 1972).

TAXONOMIC TREATMENT

Imperata Cirillo

Imperata Cirillo. Pl. Rar. Neap. 2:26. 1792.

Type species: *Imperata cylindrica* (L.) Beauv., Ess. Nouv. Agrost. 1812.

Lagurus cylindricus L., Syst. Nat. ed. 10 2:878. 1759.

Description

Plants perennial; strongly rhizomatous; culms mostly erect and unbranched, generally with few nodes; blades linear to lanceolate, mostly basal, culm blades reduced; sheaths open, often with auricular trichomes; ligule membranous, extremely variable; panicle solitary, terminal, cylindrical to conical; branches divided; rachis often with numerous long trichomes; pedicel tips cup-like; spikelets all similar, unequally pedicellate, disarticulation below glumes; glumes equal to subequal, membranous, 3-9-nerved, with long trichomes from the callus to at least the midpoint; florets 2, enclosed by glumes, lowest reduced to hyaline sterile lemma, upper with palea and lemma, and a perfect flower; lemma hyaline, 0-1-nerved, lanceolate to ovate, denticulate; palea broadly ovate, hyaline, 0-3-nerved, denticulate; lodicules 0; anthers 1-2, yellow to brown; stigmas elongate, purple to brown; styles connate to free; caryopses ovate to obovate, light to dark brown.

Discussion

Imperata forms a relatively distinct group of the Andropogoneae. The genus has been placed in the subtribe Saccharinae by Clayton (1972). Hackel (1883) split the genus into the sections Imperatella (plants with two stamens) and Eriopogon (the rest of the genus).

The exact position of the genus in relation to neighboring groups is yet unclear. Janaki-Ammal (1941) was able to produce fertile hybrids between Imperata and Saccharum. Roberty (1960) submerged Imperata in Saccharum. Clayton (1972) has noted that Eccoilopus, Imperata, Miscanthus, Miscanthidium, and Sclerostachya form a morphologically similar group (with non-disarticulating rachis and all spikelets pedicellate). The remaining portion of the Saccharastrae (Spodiopogon, Eriochrysis, Saccharum, and Narenga) have a disarticulating rachis and one sessile spikelet in each pair.

Clayton also conjectured that the "paniculate inflorescence and unspecialized spikelets with thin glumes and weakly developed awns suggest that this may be regarded as the most primitive group of the Andropogoneae. This conclusion is contradicted to some extent by the loss of function in the lower floret, and it is probably truer to say that, their obvious adaptation to wind dispersal, has led to the retention of certain primitive characters."

One character I observed which may help circumscribe generic boundaries is the presence of papillate subsidiary cells in the stomatal apparatus (Figure 15). These were found consistently on the adaxial

leaf epidermis and occasionally on the abaxial surface. An examination of numerous species (see Materials and Methods) of Erianthus, Saccharum, Miscanthus, and Eriochrysis did not reveal papillate subsidiary cells on either epidermal surface.

I have observed that most previous authors have underestimated leaf length of Imperata species, probably because of the absence of the large basal leaves on many herbarium sheets.

Key to Species of Imperata

1. Anthers two; inflorescence less than 20 cm long

    2. Ligule 0.5-2.0 mm long; pedicels elongate; plants of the Old World; introduced to southeastern United States . . . . . I. cylindrica

    2. Ligule 1.8-3.8 mm long; pedicels short; plants of Chile and Argentina . . . . . I. condensata

1. Anthers one; inflorescence of variable length

    3. Spikelets 3.0 mm or less long, blades 5 mm or narrower; one of three inner bracts (fertile lemma) may be missing; plants of South America. . . . . I. minutiflora

    3. Spikelet 3.2 mm or longer; leaves various

        4. Inflorescence 7-13 cm long, cylindrical, lower branches 1-3 cm long; plants of the New World. . . . . I. brasiliensis

        4. Inflorescence generally 15 cm or longer, lower branches 3 cm or longer; plants of the Old or New World

            5. Trichomes on spikelets 5-6 mm long; inflorescence nearly half as long as culm, plants of Kermadec Islands. . . I. cheesemanii

            5. Trichomes on spikelets 8-16 mm long; inflorescence 1/4 to 1/3 the length of the culm

6. Blades 1-5 mm wide; inner spikelet bracts 2-3 (fertile lemma may be missing); plants of South America . . . . . I. tenuis

6. Blades 5 mm or wider; inner spikelet bracts 3

7. Lower inflorescence branches 6-10 cm long; upper portion of inflorescence flexuous; plants of eastern Asia and Pacific Islands. . . . . I. conferta

7. Lower inflorescence branches 1-6 cm long; upper parts of inflorescence more rigid; plants of New World

8. Panicle loose to dense; sterile lemma hyaline; mesic areas; southern Mexico through South America. . . . . I. contracta

8. Panicle very dense; sterile lemma membranous, glume-like; desert habitats; southwestern U.S. and northern Mexico . . I. brevifolia

Imperata brevifolia Vasey

Imperata brevifolia Vasey, Bull . Torrey Bot. Club 13:26. 1886.

Type : USA, San Bernardino Valley, California, wet soils, 15 Aug 1881. Parish 1031 (US!)

Imperata hookeri Hack., DC. Monogr. Phan. 6:97. 1889.

Description

Perennial; culms erect, (51) 62-112 (129) cm tall with reduced blades; leaves mostly basal; blades linear to linear-lanceolate (7) 8-12

(14) mm wide, abaxial surface smooth, adaxial scabrous; ligule (0.7) 1.1-2.5 (2.9) mm long; panicle dense, (16.5) 17.9-26.7 (33.5) cm long; lower branches (2) 2-4 (5) cm long; trichomes from the callus and glumes (8) 8-12 (12) mm long; glumes subequal to equal (2.6) 2.7-3.7 (4.1) mm long, 3-7 nerved; sterile lemma membranous, glume-like, (2.5) 2.5-3.3 (3.9) mm long, (0.6) 0.7-0.9 (1.1) mm wide; fertile lemma hyaline, (1.4) 1.7-2.3 (2.4) mm long, (0.4) 0.4-0.6 (0.7) mm wide; palea hyaline, (1.1) 1.3-1.9 (2.0) mm long, (0.4) 0.7-1.3 (1.3) mm wide, surrounding the ovary completely; anther one, (1.3) 1.7-2.3 (2.3) mm long, yellow to orange, filament broadened at base; stigmas purple to brown, (2.1) 2.3-3.3 (4.0) mm long; styles free, (0.9) 1.3-2.3 (2.4) mm long; $2n = 20$.

Nomenclature

I. brevifolia Vasey was called I. hookeri Ruprecht ex Andersson. Ruprecht apparently never effectively published the name (Article 29, Stafleu, 1978), but according to Vasey (1886) did write the name on a specimen (Drummond II: 283.). Andersson did include the name under Imperata arundinacea, but did not designate a taxonomic rank, rather using only an asterisk before the epithet. Wheeler (1939) suggested that this may indicate Andersson intended the designation "forma" which he applied loosely. This does not meet the criteria set forth in Article 34 (Stafleu, 1978) for valid publication. Hackel (1889) used I. hookeri at specific rank, citing Andersson's earlier work. Vasey described I. brevifolia in 1886, which thus has priority over Hackel's designation (Art. 11, Stafleu, 1978), but used the name I. hookeri in 1892.

Discussion

The distribution of I. brevifolia was given by Hitchcock (1951) as "desert regions, western Texas to southern California, Utah, Nevada, Mexico." This range also is confirmed by herbarium specimens. Most specimens, however, were collected before 1945, which suggests that the species may have become rarer. As part of this study of the genus Imperata, an attempt was made to relocate old collection sites in the Southwest from herbarium data. Living stands were sought in western Texas, New Mexico, Arizona, southern Utah, and southern California. No living plants were observed except in Grand Canyon National Park (GCNP), where populations were located at Pipe Creek and Bright Angel Creek in 1981. Previous collections had been made at these and other sites in GCNP. Sites where I. brevifolia formerly was collected have been altered by intensive grazing, cultivation, construction of houses, condominiums, and trailer parks, the invasion of weedy species such as Tamarix, and the impoundment of water. The species has been collected at only one locality outside Grand Canyon in the 1970's, and that site now is under Lake Powell.

Imperata brasiliensis Trin.

Imperata brasiliensis Trin., Mem. Acad. Imp. Sci. St. Petersbourg (Ser 5) 2:331. 1832.

Type: Brasil, Minas Geraes, Serra de Lapa. Riedel 1016 (LE! K! US fragment!)

Saccharum sape Saint-Hilaire, It. Bras. II. 368. 1833.

Imperata brasiliensis var. mexicana Rupr., Acad. Sci. Brux. Bel. 9:245. 1842. Mexico, Vera Cruz. Galeotti 5678 (K! P fragment US!)

Imperata sape (St. Hil) Anderss., Ofv. Vet. Akad. Förh. 12:159. 1855.

Imperata arundinacea var. americana Anderss., Ofv. Vet. Akad. Förh. 12:160. 1855.

Imperata caudata (non Trinius) in Chapman, Fl. South U.S. ed. 2. 668. 1883.

Description

Perennial; culms erect (22) 36-74 (98) cm tall; leaves basal, blades linear-lanceolate (3) 5-13 (19) mm wide; ligule short (0.5) 0.6-1.4 (1.7) mm long; panicles relatively short (7.5) 8.3-13.3 (17) cm long, lower branches short (1) 1-2.8 (3.5) cm long; spikelets surrounded by silky trichomes (7) 8.9-11.7 (13) mm long; glumes membranous, (2.4) 3.1-4.3 (4.5) mm long; sterile lemma (1.0) 1.7-3.1 (3.4) mm long, (0.5) 0.5-0.9 (1.1) mm long; fertile lemma present or absent, if present about 1 mm long and 0.3 mm wide; palea (0.6) 0.8-1.6 (2.2) mm long, (0.4) 0.5-1.1 (1.5) mm wide; stamens one; anther (1.4) 1.6-2.4 (2.8) mm long, filament base dilated; stigmas variable, (2.4) 2.8-4.6 (6.7) mm long; style (1.1) 1.4-3.4 (4.7) mm long.

Nomenclature

Andersson (1855) included both I. arundinacea var. americana Anderss. and I. sape Anderss. in this treatment. In the description of the former, he indicated it was scarcely distinguishable from I. sape.

Discussion

In many specimens, one of the hyaline inner bracts is apparently missing. From the position of the other bracts, one may deduce that the fertile lemma is absent. Hackel (1889) also supports this conclusion. Rarely the bracts are positioned so that determination of the missing bract is not possible.

In a few specimens I have observed two stamens. In some of these the second was not fully developed.

The range of I. brasiliensis includes South America, Central America, southern Mexico, Cuba, and Florida. It is abundant in many areas in Brazil and has become weedy (Aronovich et al., 1973).

Imperata brasiliensis is often confused with I. cylindrica with which it is allied. Inflorescence shape is approximately the same. Differences include stamen number and number of bracts within the glumes. I. brasiliensis is usually smaller, with shorter culms, inflorescences and leaves.

Imperata cheesemanii Hack.

Imperata cheesemanii Hack., Trans. Proc. New Zealand Inst. 35:378-379. 1903.

Type: Kermadec Islands, Aug 1884

Cheeseman 1001 (US!)

Description

Perennial; culms erect, (34) 34-55 (60) cm tall; leaves mostly basal; blades (9) 10.1-13.5 (14) mm wide, linear to lanceolate, narrowing

greatly at base; ligule relatively short (1.1) 1.1-2.5 (2.9) mm; panicle nearly half as long as culm (15.5) 15.5-21.2 (22.5) cm, light brown; lower branches (2.0) 2.0-3.7 (4.5) cm long; trichomes on glumes (5.0) 5.0-5.8 (6.0) mm long; glumes subequal, (2.7) 2.8-3.4 (3.7) mm long, inconspicuously 3-5-nerved; sterile lemma (1.9) 2.0-2.2 (2.3) mm long, (0.7) 0.8-1.3 (1.3) mm wide, hyaline; fertile lemma (1.9) 2.1-2.5 (2.6) mm long, (0.6) 0.6-0.8 (0.8) mm wide; palea (0.9) 1.0-1.5 (1.5) mm long, (0.6) 0.6-1.2 (1.2) mm wide, surrounding ovary; in some spikelets four inner bracts were observed; stamen one; anther (1.7) 1.8-2.2 (2.2) mm long; stigmas (2.2) 2.4-3.2 (3.3) mm long; styles (1.4) 1.6-2.0 (2.1) mm long, fused for half their length.

Discussion

Imperata cheesemanii Hack. is closely allied to I. conferta Ohwi. It has been found only in the Kermadec Islands. This small group of islands lies north of New Zealand (1000 km north of Auckland). I. cheesemanii is easily distinguished from I. conferta by the extremely short trichomes on the spikelet. This gives the inflorescence a light brown color rather than the typical silky white color of Imperata species. The inflorescence does not have the elongated basal branches of I. conferta. Also, the inflorescence is nearly half the length of the culm, whereas other Imperata panicles reach only one-third to one-fourth of the culm length. Plants of this species consistently clustered separately in both the PCA and the cluster analysis. Living material is not yet available for chromosome or electrophoretic analysis.

Hubbard (1944) gave the date of publication of I. cheesemanii Hack. as 1893. This seems to be in error. Chase and Niles (1962) cite a 1902 letter from Hackel to Cheeseman acknowledging grasses from Cheeseman including "Imperata cheesemani Hack. n. sp."

Imperata condensata Steud.

Imperata condensata Steud., Syn. Pl. Glum. 1:431. 1855.

Type: Chile, Cordilleras de Ranco. Lechler 831 (US!)

Imperata arundinacea var. condensata (Steud.) Hack., DC. Monogr. Phan. 6:94. 1889.

I. cylindrica var. condensata (Steud.) Hack. ex Stuckert, Anal. Mus. Nac. Buenos Aires 21:9. 1911.

Description

Perennial; culms erect, (19) 27-55 (69) cm tall; blades short, linear-lanceolate (3.0) 4.7-9.7 (11.0) mm wide, leaf tips very narrow; ligule (1.5) 1.9-3.7 (4.5) mm long; panicle compact, (7.0) 7.5-12.1 (14.0) cm long, lower branches shortened (1.0) 1.0-2.0 (2.0) cm long, pedicel apex cup-like, pedicels short; spikelet trichomes (8.0) 9.6-15.2 (16.0) mm long; glumes subequal to equal (2.7) 3.3-4.3 (4.5) mm long, 3-9-nerved; sterile lemma (1.9) 2.4-3.8 (4.0) mm long, (0.9) 0.9-1.3 (1.4) mm wide; fertile lemma (0.9) 1.5-2.1 (2.1) mm long, (0.4) 0.5-0.9 (1.0) mm wide; palea (1.2) 1.2-1.8 (2.0) mm long, (0.8) 0.9-1.3 (1.4) mm wide; stigma (2.7) 2.9-3.5 (3.9) mm long, brown to purple; style (2.1) 2.2-3.2 (3.7) mm long, styles fused less than half of length.

Discussion

I. condensata is native to Chile and western Argentina. It is very similar to I. cylindrica of the Old World, being differentiated from it by the contracted inflorescences, broad cup-like apex of the pedicels, long ligules and finely pointed leaves. Some plants I observed are small, possibly as a result of environmental conditions.

Acevedo (1968) indicated that the range of I. condensata extended to Tierra del Fuego. I have not seen any plants that were collected beyond 45° S. Acevedo also indicated that the holotype at B was destroyed.

Imperata conferta (Presl) Ohwi

Imperata conferta (Presl) Ohwi, Bot. Mag. Tokyo 55:549. 1941.

Type: Philippines, Luzon Haenke (s.n.) (US!) Saccharum confertum Presl, Rel. Haenk. 1:346. 1830.

Imperata exaltata (Roxb.) Brongn. in Duperrey Bot. Voy. Coq. 22:101. 1831. pro parte

Imperata exaltata var. genuina Hack., DC. Monogr. Phan. 6:98. 1889 (US! K!)

Imperata exaltata subsp. merrillii Hack., Philipp. J. Sci. 1:264. 1906. (US!)

Description

Perennial; culms (44) 68-116 (146) cm tall; leaves basal; blades linear-lanceolate, (5.0) 10.3-17.7 (20.0) mm wide, both sides glabrous; ligule (0.5) 0.8-1.2 (1.6) mm long; upper leaves reduced; panicle nearly conical, the upper rachis very thin and flexible, lower branches elongate

(1.0) 5.6-11.0 (14.0) cm long and spreading; pedicels long and slendar; spikelet trichomes (6) 10-12 (13) mm in length, glumes subequal, membranous, (2.3) 2.6-3.2 (3.5) mm long, 3-5-nerved; sterile lemma (1.4) 1.6-2.2 (2.6) mm long, (0.4) 0.6-1.0 (1.2) mm wide; fertile lemma (1.3) 1.6-2.2 (2.5) mm long, (0.3) 0.3-0.5 (0.7) mm wide; palea (0.9) 0.9-1.3 (1.6) mm long, (0.4) 0.7-1.1 (1.3) mm wide; anthers 1, yellow to orange, (1.4) 1.4-2.2 (2.7) mm long; stigmas purple, (1.2) 1.4-2.4 (3.6) mm long; styles fused from half to their full length, (0.9) 1.1-1.9 (2.7) mm long; 2n = 20.

Nomeclature

In 1814, Roxburgh published the name Saccharum exaltatum. Later (1820), he published the name and a description, indicating the plant was a native of India. No specimens were cited. If the plant(s) he described were actually Imperata, it seems likely from this distribution that S. exaltatum is I. cylindrica. Brongniart (1831) based I. exaltata on Roxburgh's treatment and included a brief description, but cited no specimens. Although the date on the title page is 1829, the actual publication date was 1831 (Stafleu and Cowan, 1976). Hackel (1889) indicated that Saccharum exaltatum Roxb. was actually S. arundinaceum Retz., not an Imperata. Hackel did accept the name I. exaltata Brongn., sensu stricto. Hackel (1889) split I. exaltata into three varieties. His var. genuina (Cuming 1801!, 2411!, Haenke s.n.!) fits the concept of Saccharum confertum Presl. Ohwi (1941) authored Imperata conferta based upon Presl's (1830) description of S. confertum.

Even though Presl's description is unclear, the locality (Sorzogon, Luzon) in the Philippines is well within the range of I. conferta. The publication date of 1830 also has priority over I. exaltata Brongn.

Discussion

These plants are found in open areas, beaches, old fields, clearings, landslides, etc., on sandy or clay soils. The range extends from the Malay peninsula through the Philippines, and other Pacific Islands. The western part of the range overlaps with that of I. cylindrica. It is likely that some hybridization occurs between these two groups. This may be a partial explanation for the confusion in the literature.

Hackel (1906) indicated that the culms of both I. exaltata Brongn. and I. exaltata Brongn. subsp. merrillii are hollow, but culms of all other species of this genus are solid. This is not true. I have observed both solid and hollow culms in all species. The hollowness of the culm seems to be correlated with age rather than species, as young culms of all taxa are solid, and old culms of all species are generally hollow. There is also a gradient from top (solid) to bottom (hollow) within one culm.

Hackel differentiated I. exaltata subsp. exaltata and subspecies merrillii by leaf and inflorescence shape. He indicated the spikelets were identical. I have noticed that leaf shape and inflorescence shape are quite variable within the geographic and altitudinal range of the species. The type of I. exaltata subsp. merrillii (Merrill 4813!) has narrow leaves. This is but a variant of I. conferta Ohwi.

In 1974, Williams et al. studied flavonoid distribution in Saccharum and related genera. They found great differences between Imperata cylindrica and I. conferta. Using their presence-absence data, it appears that I. conferta is more closely related to species of Sclerostachya, Miscanthus and Saccharum than it is to I. cylindrica.

Imperata contracta (H. B. K.) Hitchc.

Imperata contracta (H. B. K.) Hitchc., Ann. Rep. Missouri Bot. Gard. 4:146. 1893.

Type: Colombia, fluvii Magdalenae. St. Hilaire (P, US!)

Saccharum contractum H. B. K., Nov. Gen. & Sp. 1:182. 1816.

Saccharum dubium H. B. K., Nov. Gen. & Sp. 1:183. 1816. (US!)

Saccharum caudatum G. Meyer, Prim. Fl. Esseq. 68. 1818.

Anatherum caudatum Schult., Mant. 2:445. 1824.

Anatherum portoricense Spreng., Syst. Veg. 1:290. 1825.

Imperata caudata Trin., Mem. Acad. Imp. Sci. St. Petersb. 6:331. 1832.

Imperata exaltata var. caudata Hack., DC. Monogr. Phan. 6:99. 1889.

Description

Perennial; culms erect, unbranched, (42) 71-131 (149) cm tall; leaf blades reduced on culm, long, mostly basal (5.0) 6.6-10.6 (12.0) mm wide, base narrow; ligule U-shaped or V-shaped, (0.4) 0.8-1.8 (2.4) mm long; panicle elongate (8.0) 15.0-41.1 (55.0) mm long, branches somewhat appressed (3.0) 3.3-6.1 (8.0) mm long; spikelet trichomes (8.0) 8.2-10.4 (11.0) mm long, glumes (2.1) 2.4-3.2 (3.7) mm long, subequal,

3-5-nerved; sterile lemma (0.5) 0.6-0.8 (0.9) mm wide, (0.7) 1.2-2.4 (3.5) mm long; fertile lemma (0.4) 0.6-1.2 (1.6) mm long, (0.1) 0.2-0.4 (0.6) mm wide; palea (0.6) 0.8-1.2 (1.4) mm long, (0.5) 0.6-0.8 (0.9) mm wide; anther 1, (1.2) 1.3-1.9 (2.5) mm long, yellow to orange-brown; stigma (1.4) 1.9-2.9 (3.7) mm long; style (1.0) 1.1-1.7 (2.1) mm long, often bifurcate at length; $2n = 20$.

Nomenclature

In 1816, Humboldt et al. described Saccharum contractum and S. dubium. Descriptions of the two fall within the variation present in Imperata contracta. Locations of the two Saccharum species described are the same, with blooming time listed as May and September for the former, and July for the latter. Imperata contracta has a long blooming period. Pohl (1980) indicates that blooming may occur year long. Herbarium labels I have seen as well as greenhouse studies support Pohl.

Humboldt et al. (1816) listed S. polystachyum Swartz in synonomy with S. dubium. I have seen a fragment (US 1448358) taken by Chase from "Herb. Beauvois." "St. Dominique" and "P. B. script" are also on the label. The fragment is I. contracta.

Meyer (1818) described S. caudatum from Essequibo (British Guiana). He cited S. contractum H. B. K. as "valde affine." I have seen a specimen labelled "Imperata caudata M." and "surinam ex Hb Reich. ex Trin hb" which is probably type material of S. caudatum Meyer (US 81720).

Trinius (1832) gave a brief description of I. caudata. In synonomy, he cited S. caudatum Meyer and S. contractum. No specimens were cited.

Discussion

These plants are weedy in nature, occurring along river and stream banks, as a weed in cleared land, and on roadsides. The plants seem to have a relatively high moisture requirement, as most labels with habitat data indicate "wet places." The range of I. contracta extends from southern Mexico to Argentina with greater frequency in northern South America. The species is morphologically quite variable. This taxon is obviously allied with I. brevifolia and I. conferta.

Imperata cylindrica (L.) Beauv.

Imperata cylindrica (L.) Beauv., Ess. Nouv. Agrost. 7. 1812.

Lagurus cylindricus L., Syst. Nat. ed. 102:878. 1759.

Saccharum cylindricum (L.) Lam., Encycl. 1:594. 1783.

Saccharum laguroides Pourr., Mem. Acad. Sci. Toulouse 3:326. 1788.

Saccharum koenigii Retz., Obs. Bot. 5:16. 1789.

Saccharum thunbergii Retz., Obs. Bot. 5:16. 1789.

Imperata arundinacea Cirillo, Pl. Rar. Neap. 2:27. 1792.

Saccharum sisca Cav., Icon 3:47. 1794.

Calamagrostis lagurus Koel., Desc. Gram. 112. 1802.

Saccharum cylindricum europaeum Pers., Syn. Pl. 1:103. 1805.

Imperata thunbergii (Retz.) Beauv., Ess. Nouv. Agrost. 165. 1812.

Imperata koenigii (Retz.) Beauv., Ess. Nouv. Agrost. 165. 1822.

Imperata sieberi Opiz, Natural. 10:190. 1825.

Imperata allang Jungh., Tijdschr. Nat. Gesch 7:295. 1840.

Imperata koenigii var. maior Nees, Fl. Afr. Austr. 1:90. 1841.

Imperata pedicellata Steud., Flora 29:22. 1846.

I. arundinacea var. glabrescens Büse, Pl. Jungh. 366. 1854.

I. arundinacea var. indica Anderss., Ofv. Vet. Akad. Forh. 12:160. 1855.

I. arundinacea var. europea Anderss., Ofv. Vet. Akad. Forh. 12:160. 1855.

I. arundinacea var. africana Anderss., Ofv. Vet. Akad. Forh. 12: 159. 1855.

I. arundinacea var. koenigii (Retz.) Benth., Fl. Hongk. 419. 1861.

I. arundinacea var. pedicellata (Steud.) Debeaux, Rech. Fl. Pyrenees Oriental 323. 187.

I. arundinacea var. koeniggi subvar. glabrescens (Büse) Hack., DC. Monogr. Phan. 6:95. 1889.

I. arundinacea var. latifolia Hook., Fl. Brit. Ind. 7:106. 1896.

Imperata cylindrica var. europea (Anderss.) Aschers. & Graebn., Syn. Mitteleur. Fl. 1:412. 1898.

Imperata angolensis Fritsch, Bull. Herb. Boiss. II. 1:1096. 1901.

Imperata cylindrica var. koenigii (Retz.) Pilger, Fragm. F. Phil. 137. 1904.

Imperata cylindrica var. genuina (Hack.) A. Camus, Rev. Bot. Appl. 5:110. 1925.

Imperata cylindrica f. pallida Honda, J. Fac. Sci. Univ. Tokyo Sec. III. Bot. 3:374. 1930.

Imperata cylindrica var. major (Nees) C. E. Hubbard, Grass., Maurit., Rodrüguez 96. 1940.

Imperata cylindrica var. africana (Anderss.) C. E. Hubbard, Joint Pub. Imp. Ag. Bur. 7:10. 1944.

Imperata cylindrica var. latifolia (Hook.) C.E. Hubbard, Joint Pub. Imp. Ag. Bur. 7:10. 1944.

Description

Perennial; culms erect, (10) 31-95 (217) cm tall, thin to thick and stiff; leaf sheaths may have auricular trichomes, blades linear-lanceolate, narrowing to broad midrib at base, (1) 3-11 (28) mm wide, short to 150 cm long, upper blades much reduced; ligule variable in shape and texture, (0.2) 0.7-1.7 (3.5) mm in length; panicle spike-like, cylindrical, (3.5) 5.7-22.3 (52.0) cm long, lower branches (1.0) 1.0-3.2 (7.0) cm long, trichomes on spikelet (9.0) 11.2-12.6 (16.0) mm long, glumes lanceolate to ovate, (2.6) 3.1-4.5 (5.5) mm long, equal to subequal, thicker toward the base, 3-9-nerved; sterile lemma hyaline, denticulate (1.4) 1.8-3.6 (4.5) mm long, (0.5) 0.8-1.4 (2.1) mm wide; fertile lemma similar, (0.7) 1.3-2.3 (3.4) mm long, (0.3) 0.5-0.9 (1.8) mm wide; palea similar (0.6) 1.1-1.9 (2.8) mm long, (0.5) 0.8-1.4 (1.8) mm wide; anthers 2, orange to brown, (1.5) 2.2-3.2 (4.2) mm long; stigmas purple to brown, (1.7) 2.8-5.2 (8.3) mm long; styles fused at length to free, (0.5) 1.5-2.7 (3.4) mm long; caryopsis light to dark brown.

Nomenclature

Lagurus cylindricus was described by Linnaeus in 1759. The specimen at LINN labelled L. cylindricus (96.2) is I. cylindrica. Unfortunately, there is no evidence that Linnaeus observed the specimen. The handwriting on the specimen was unrecognized by Savage (1945).

Also at LINN are plants labelled Saccharum spicatum (77.5-77.7). Savage (1945) indicated the script on these specimens was that of Sir James E. Smith. The last two also have the writing of Thunberg. All

three plants were I. cylindrica. Linnaeus described S. spicatum in 1753. If these were the plants he described at that time, then the epithet spicata would have priority. There is no evidence that Linnaeus saw these plants. Aiton (1789) indicated the Linnaean description and citation of Plukenet (1696) referred to Perotis latifolia. Chase and Niles (1962) cited a letter from Stapf indicating "a sample (of Plukenet's specimen) in Morison's (herbarium) is Melica ciliata." "Melica ciliata L. is not found in India but the closely related M. cupani is in India."

Lamarck (1783) cited Linnaeus in his description of Saccharum cylindricum. Retzius (1789) described Saccharum koenigii and S. thunbergii. He cited in synonomy S. spicatum of Thunberg.

If Linnaeus did not use the specimens now at LINN, a problem of typification arises. It would be possible to choose the LINN material or other collections (possibly Retzius' S. thunbergii or S. koenigii) as neotypes. Without a great amount of detective work to determine if all specimens seen by Linnaeus were destroyed, a neotype should probably not be selected.

Cirillo (1792) was the first author to use the name Imperata. He named the genus in honor of Ferante Imperato of Naples. He did cite Linnaeus' L. cylindricus, but used the specific name Imperata arundinacea.

Raeuschel (1797) was the first author to use the combination Imperata cylindrica. It is obvious that he knew of Cirillo's 1792 Plantarum Rariorum Regni Neapolitani, for he indicated I. cylindrica occurred in Regn. neap." Kerguelen (1978) has indicated that Raeuschel

should be cited as the author of I. cylindrica. I do not agree. Raeuschel did not cite Cirillo, or Linnaeus. This does not seem to qualify as an indirect reference as stated in Article 32 of Stafleu (1978).

Beauvois (1812) accepted the generic name of Cirillo and cited "Laguri" of Linnaeus. He also disclosed his concept of the genus through a listing of synonomy which transferred a number of Saccharum species to Imperata.

Discussion

I. cylindrica is the most variable species in the genus. The plants occur from the western Mediterranean to South Africa, through India, Southeast Asia, and Pacific Islands to Australia. It has been introduced to the southeastern United States in this century. As might be expected, a group of plants with such a wide geographic range would also have much morphological variability.

This variability has resulted in a proliferation of names for representatives of the taxon. Andersson (1855) and Hackel (1889) included many subspecific taxa in their treatments of I. arundinacea. Hubbard (1944) described five varieties. Imperata cylindrica var. europaea (Anderss.) Aschers. & Graebn. is said to be present around the Mediterranean, in North Africa, and east to Afghanistan. Roux and Adjanohoun (1958) reported a chromosome number of 2n = 40 for plants of this group. I. cylindrica var. africana (Anderss.) C. E. Hubbard is reported as present throughout central and southern Africa. Roux and Adjanohoun (1958) reported 2n = c 60 for this group. Imperata cylindrica

var. major (Nees) C. E. Hubbard was said to range from East Africa through India, Southeast Asia, Pacific Islands (including Japan), and Australia. Chromosome counts of 2n = 20 have been reported several times. I. cylindrica var. latifolia was said to occur only in the northern part of the United Provinces of India. Hole (1911) reported that this robust variety grows in area where moisture is abundant. Bor (1941) has described some of the variability present in the species in India.

The above varieties of I. cylindrica probably reflect some actual differences within the species. It is possible to separate statistically some individuals which could be assigned to these groups, but identification of any one specimen to variety without knowing its geographic origin is very difficult. Hubbard (1944) did not include a key to his varieties. It would be impossible to construct a workable key to varieties if ranges of variation within each variety were considered. For this reason, I do not recognize varieties of I. cylindrica.

I. cylindrica is notorious as a weed in most parts of its range. Holm et al. (1977) have included it among the 10 worst weeds of the world. One of the greatest problems is the shifting agricultural patterns in many tropical regions which provide conditions favorable to the weed. Westing (1971) reported that military defoliation in Southeast Asia has encouraged the spread of the weed. Gray (1944) and Holm et al. (1977) have compiled lists of crops which have been infested with the weed. Included are rubber, citrus, tea, and coconut crops. The spread of I. cylindrica in the southeastern United States has been documented by Dickens (1974) and Patterson et al. (1981).

I. cylindrica is a well adapted weed. It spreads aggressively by its rhizomes and is capable of sexual reproduction. The plants prosper in a wide variety of environmental conditions and in poor soils.

In recent years, a number of studies on Imperata control have been reported. These include publications by Soerjani (1970), Soerjani and Soemarwoto (1969), Sukartaatmadja and Siregar (1971), and Eussen et al. (1976). Eussen (1978) has also presented evidence which indicates allelopathic effects in Imperata cylindrica.

In addition to its detrimental weediness, Imperata cylindrica may be a host to a variety of plant pathogens. Included are Ephalis oryzae (Govindu, 1969), Helminthosporium sacchari (Mishra et al., 1973), Xanthomonas albideans (Ryan, 1976), Tetraneura radicicola (Rai, 1975), and Aphanisticus penninsula (Manley, 1977).

Several attempts have been made to find uses for the abundant I. cylindrica. Soewardi et al. (1974) studied its utility as a cattle feed. Generally it is not palatable to cattle except when the plants are young. Pendelton (1948) stated that the plants could help prevent soil erosion. Brown (1944) has discussed its use for papermaking, mulch, thatch, packing material, pillows, bedding, fuel, and medicine.

Lists of common names of I. cylindrica have been compiled by Hubbard (1944) and Holm et al. (1977).

Imperata minutiflora Hack.

Imperata minutiflora Hack. DC. Monogr. Phan. 6:100. 1889.

Type: Peru, Lima, Barranca 524. (US!)

Description

Perennial; rhizomes slender; culms often branched, slender, (21) 34-98 (125) cm tall; leaf blades narrow, (3) 3-6 (10) mm wide, linear-lanceolate, adaxial surface covered with prominent papillae; ligule minute, (0.3) 0.3-1.1 (1.4) mm long; panicle narrow, (13.5) 14.7-26.5 (34.5) cm long, nodding slightly; lower branches (2.0) 2.0-4.3 (6.0) cm long; spikelet trichomes (1.0) 4.8-8.6 (9.0) mm long; spikelets short; glumes subequal (1.5) 1.5-2.7 (3.3) mm long; sterile lemma (0.9) 1.2-1.6 (1.7) mm long, (0.3) 0.4-0.6 (0.8) mm wide; fertile lemma may be missing or reduced; palea (0.5) 0.7-1.1 (1.2) mm long, (0.3) 0.4-0.8 (0.8) mm wide, completely surrounding the ovary; anther 1, yellow to orange, (0.9) 1.0-1.4 (1.7) mm long; stigmas (1.0) 1.0-2.0 (2.3) mm long, purple to dark brown; styles (0.5) 0.6-1.4 (1.8) mm long, free.

Discussion

Imperata minutiflora is one of the most distinctive species of the genus. This is the only group with branching culms and small rhizomes. Spikelets are much smaller than other taxa. The papillae on the adaxial surface of the leaf blade are readily visible with a handlens.

Specimens I observed were collected along watercourses and roadsides.

The range of I. minutiflora extends from northern Argentina through Bolivia, Peru, and Ecuador.

Imperata tenuis Hack.

Imperata tenuis Hack., DC. Monogr. Phan. 6:689. 1889.

Type: Brasil, Minarum Glaziou 17442 (W US!)

Description

Perennial; culms erect, (59) 68-110 (126) cm tall, leaves basal; blades narrow (2.0) 2.9-4.7 (5.0) mm wide, culm blades reduced; ligule variable, (0.8) 1.2-3.0 (3.3) mm long; panicle narrow, (13.0) 14.7-24.5 (28.5) cm long; lower branches (2.0) 2.0-3.4 (4.0) cm long; spikelet trichomes (8.0) 8.7-10.9 (11.0) mm long; glumes subequal, (2.5) 3.0-4.0 (3.9) mm long; sterile lemma (0.9) 1.3-2.3 (2.4) mm long, (0.3) 0.3-0.7 (0.9) mm wide; fertile lemma may be absent; palea (0.8) 0.9-1.3 (1.3) mm long, (0.6) 0.7-1.1 (1.2) mm wide; anther 1, orange to brown, (1.2) 1.5-2.3 (2.4) mm long; stigmas dark, (1.1) 1.2-2.0 (2.2) mm long.

Discussion

These plants show affinities to I. minutiflora and I. brasiliensis. The inflorescence is narrow and slightly flexuous toward the tip. Leaf blades are extremely narrow.

The plants are found most frequently in wet areas and along watercourses. Their range includes northeastern Argentina, the Mato Grosso of Brazil and Bolivia. I have not seen any plants from Paraguay, but it is likely they are present in that country.

DISCUSSION

Data from morphological measurements, anatomical studies, chromosome analysis, electrophoresis, and numerical analysis were used in studying the genus Imperata. Some of the taxa (I. cylindrica, I. conferta, I. brasiliensis) were shown to have a great deal of variability. Characters of the taxa often overlap, making identification difficult.

Hartley (1958) has discussed the evolution of the Andropogoneae. He noted that centers of distribution of the tribe are in India and Indonesia. These areas are also characterized by the presence of many primitive members of the tribe (e.g., Miscanthus).

Bews (1929) considered the Saccharinae primitive in the tribe. Clayton (1972) hints at the same conclusion. Hartley (1958) said the presence of Miscanthidium in Africa indicates the early spread of the Andropogoneae, or possibly that this was the site of origin of the group.

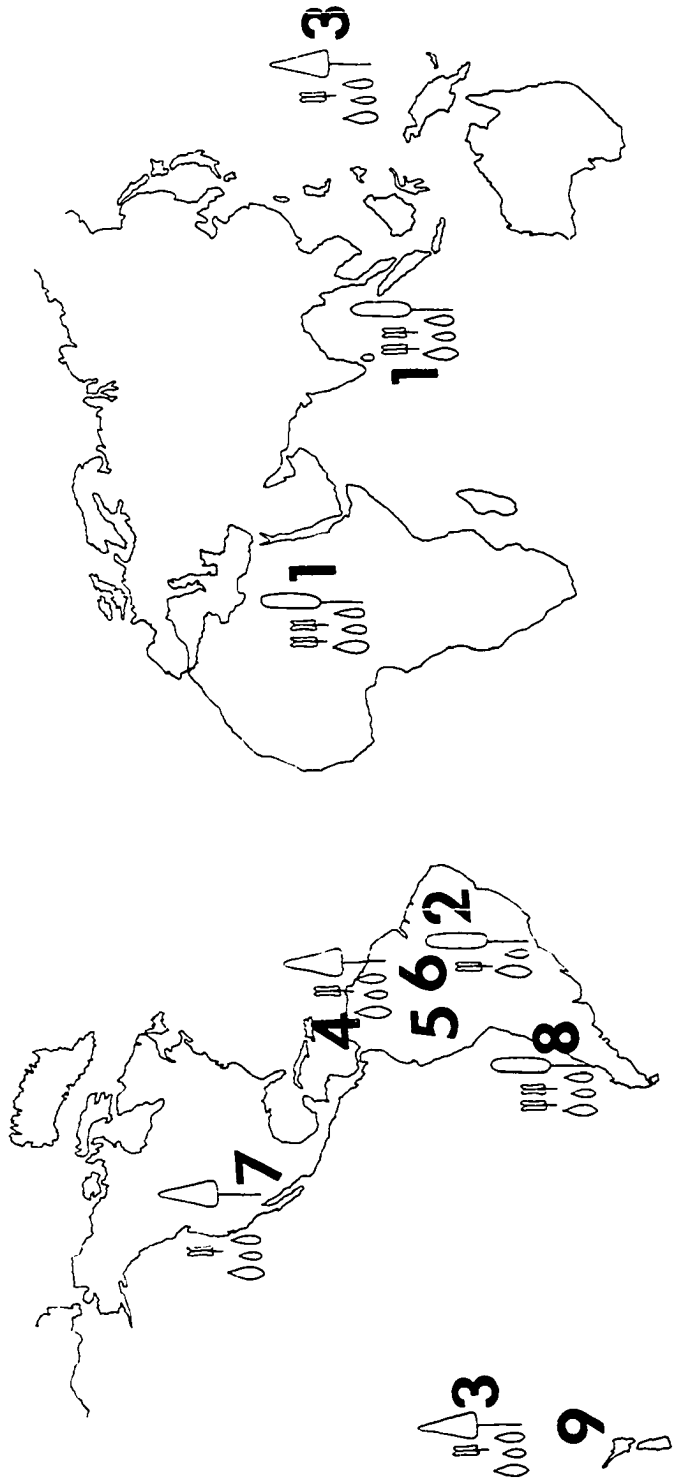
The Saccharinae include Imperata. If their origin was in southern Asia with other primitive Andropogonoids, then I. cylindrica (or a similar ancestor) is probably the most primitive species in the genus. This concept may be supported by the presence of two stamens in this species (Figure 31) which is probably more primitive than one stamen.

The Asian I. cylindrica (group 1) have $2n = 20$. Known chromosome counts for I. cylindrica in Africa and the Mediterranean are $2n = 60$ and $2n = 40$, respectively. It seems likely that these groups have been derived from the Asian stock.

Imperata cylindrica ranges east from Asia to Australia and the Pacific Islands. Its range overlaps that of I. conferta (group 3) which extends east from the Malay peninsula and has only one stamen.

A map indicating general distribution of species (Figure 31) shows that most taxa of Imperata are found in the western hemisphere. It seems likely that Imperata can survive oceanic voyages either as caryopses carried by animals (Ridley, 1930) or by floating rhizomes. Ridley (1930) reported living I. cylindrica which had washed ashore at Cocos Keeling Island probably came from Java, a distance of 700 miles. Imperata may have reached the New World by the same means.

Figure 31. Distribution of Imperata species. Diagrams show inflorescence shape, stamen number, and floret bracts. 1 = I. cylindrica, 2 = I. brasiliensis, 3 = I. conferta, 4 = I. contracta, 5 = I. minutiflora, 6 = I. tenuis, 7 = I. brevifolia, 8 = I. condensata, and 9 = I. cheesemanii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