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Gatersleben, Oct. 2, 1985

Dear Dr. Löve,

this is to inform you that the manuscript entitled

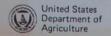
WANG, Diploid Perennial Intergeneric Hybrids in the Tribe Triticeae. II. Hybrids of Thinopyrum elongatum with Pseudoroegneria spicata and Critesion violaceum

submitted for publication in 'Biologisches Zentralblatt' has been received. Thank you very much for sending the paper. If the paper will be accepted we will contact Dr. WANG directly. - Many greetings from Prof. Rieger.

Sincerely yours

Ilse Neumann Secretary to the Managing Editors

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Agricultural Research Service Mountain States Area Crops Research Laboratory Utah State University Logan, UT 84322-6300

September 19, 1985

Dr. Askell Löve 5780 Chandler Court San Jose, CA 95123

Dear Askell:

Enclosed please find the original and two copies of my manuscript "Diploid Perennial Intergeneric Hybrids in the Tribe Triticeae. II. Hybrids of Thinopyrum elongatum with Pseudoroegneria spicata and Critesion violaceum," for your review and consideration for publishing it in the Biologisches Zentralblatt. If changes are needed for conforming to the style requirements of the Journal, please let me know.

I would appreciate receiving your words as to its acceptability for publication in the Journal before October 8 or as soon as possible. It will be helpful for my promotion which will be evaluated on October 23.

Thank you for your consideration. Best regards.

Sincerely,

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RICHARD R-C. WANG Research Geneticist

Enclosures

Dr. Richard R-C. Wang, Crops Research Laboratory, Utah State University, Logan, Utah 84322-6300.

Dear Richard:

in the tribe Triticeae. II. Hybrids of Thinopyrum elongatum with Pseudoroegneria spicata and Critesium violaceum? has arrived. As promised, I read it critically at once, and since it is good in every respect, I did not hesitate to send it to the editors of the Biologisches Zentralblatt for speedy publication with my strongest recommendation as one of their Editorial Board members. Naturally, I cannot guess when it will be printed, but my experience of earlier papers so recommended convinces me that the two outstanding cytogeneticists who are the editors of this oldest of cytogenetical journals will likely review it at

Distince themselves in addition to one more Editorial Board member from somewhere the editor, that they will agree with my positive judgement I do not hesitate to guess. I suppose they will contact you directly to tell you of the likely date of its printing.

The manuscript of your paper on @ Diploid perennial intergeneric hybrids

Your speculations as to the age andrelationship of the haplomes you study in this paper please me, since combining the cytological, morphological and, especially, geographical knowledge, I came some few years ago (still unpubl.) that instead of Doug*s morphological guess of Psathyrostchys as the most primitive group, the oldest genus must be Critesion with its Haplome, followed by Psatdoroegneria (5), Lophopyrum (J), and Thinopyrum (E) that lead to the wheat haplomes B, D and A...whereas at least most of the other haplomes seem to be dead end development of smaller branches at various parts of the main line, as far as I dare to guess now. Your continued studies will soon permit the drawing of a phylogenetic tree of much greater significance than earlier such ventures, and also for great significance for future polyploidy breeders.

With the very best regards and all good wishes,

Yours sincerely,

Askell Löve

San José, September 23, 1985.

Professor Dr. R. Rieger, Zentralisspitut für Genetik und Kulturpflanzenforschung, Akademie der Wissenschaften der BDR, DDR-4325 Catersleben, Krs. Aschersleben, East Germany.

Dear colleague:

At long last I am able to send you fine manuscript from one of our energetic and skilled Chinese-American colleagues, who is doing excellent work on studies of the diploid wheatgrasses. I have read it critically and with considerable interest and made on it some minor adjustments. And I do not hesitate to give it a strong recommendation for a speedy printing in Biologisches Zentralblatt, since I find it to be well-written and straight to the point and to comprise observations of evolutionary and future plantbreeding importance. I hope this will only be his first paper to be sent to our good old journal, and that it will stimulate his young and skilled colleagues also to send you their interesting manuscripts that

I am sure that you will help in translating his summary to a good German Zusammanfassung, since I hesitate to trust my own slowly rusting knowledge in writing German that I learned in Iceland almost half a century ago and rarely had an opportunity to use, except in reading.

With the very best regards and all good wishes, also to other friends and colleagues at Gatersleben.

Yours sincerely.

Askell Löve.

SUMMARY

Two new intergeneric hybrids involving diploid Thinopyrum elongatum were synthesized. The hybrid T. elongatum X Pseudoroegneria spicata ssp. inermis with the JeS genome formula had spikes somewhat intermediate to those of the parents. Spikes of the T. elongatum X Critesion violaceum hybrid, which has the JeHV genome combination, did not resemble those of either parent. Meiotic metaphase I showed an average of $9.13^{\mathrm{I}} + 2.35^{\mathrm{II}} + 0.05^{\mathrm{III}}$ for T. elongatum X P. spicata and 10.07^{I} + 1.86^{II} + 0.06^{III} for T. elongatum X C. violaceum. Both hybrids had many laggards at anaphase I and many micronuclei in the tetrads, and both hybrids were completely sterile. Karyotypes of root-tip cells of both hybrids fit the hypothetical ones, thus demonstrating the usefulness of karyotypes in identifying putative intergeneric hybrids. The meiotic chromosome pairing in these hybrids and the P. spicata X C. violaceum hybrids suggests that the S haplome is closer to HV than to Je and that Je is farther diverged from HV.

Significance of these two new hybrids are discussed.

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Key words: Meiosis, karyotype, genome, phylogenetic relationship, embryo

culture.

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INTRODUCTION

Many important forage grasses in the tribe Triticeae are allotetraploids, such as Elymus trachycaulus (Link) Gould ex Shinners (slender wheatgrass), E. lanceolatus (Scribner & Smith) Gould (thickspike wheatgrass), Leymus cinereus (Scribner & Merr.) Å. Löve (Great basin wildrye), and L. triticoides (Buckl.) Pilger (beardless wildrye). The species in Elymus have the genome combinations of SH, SY, or SHY where S, H, and Y are designations for the haplomes (basic genomes, Heilbronn and Kosswig, 1966) from Pseudoroegneria, Critesion, and an unknown source, respectively (Dewey 1984). Thinopyrum and the N haplome of Psathyrostachys (Dewey 1984). Therefore, wide hybridization followed by amphiploidy has played an important role in the speciation of those perennial grasses. Certainly, plant breeders can attempt to mimic nature by synthesizing new genomic combinations to create new forage species.

Thinopyrum elongatum (Host) D. R. Dewey [= Agropyron elongatum (Host) & Beauvois; Elytrigia elongata (Host) Nevski; and Lophopyrum elongatum (Host)
Â. Löve] is a diploid species having high salt tolerance (McGuire and Dvořák 1981). It has been hybridized with Aegilops squarrosa L. [= Triticum tauschii (Cosson) Schmalh.] (Dvořák 1971) and Thinopyrum bessarabicum (Savul. & Rayss) Á. Löve (= Agropyron bessarabicum Savul. & Rayss) (Wang 1985b). Because of the similarity in karyotypes of T. bessarabicum and T. elongatum and the ability of their chromosomes to pair in meiosis, it was proposed that the haplome in T. elongatum be changed from E to Je (Wang 1985b).

Continuing the series presenting data on the newly synthesized diploid intergeneric hybrids involving perennial species (Wang 1984), 1986), this paper reports the successful hybridization of T. elongatum with

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Pseudoroegneria spicata ssp. inermis (Scribner & Smith) A. Löve and		
Critesion violaceum (Boiss. & Hohenacker) Á. Löve. The spike morpho		
and cytology, both mitotic and meiotic, of the F_1 hybrids are present	ted.	

<u>Pseudoroegneria</u> <u>spicata</u> ssp. <u>inermis</u> has the S haplome and \underline{C} . <u>violaceum</u> has the H^V haplome. Thus the two hybrids reported here represent the first synthetic J^eS and J^eH^V genomic combinations.

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MATERIALS AND METHODS

The Thinopyrum elongatum accession (originally from the Mediterranean coast of France) was received from Dr. Y. Cauderon of I.N.R.A., Versailles, France. Pseudoroegneria spicata ssp. inermis (PI 236670), from Alberta, Canada, and Critesion violaceum (PI 401390) from northcentral Iran, were provided by the USDA Regional Plant Introduction Station, Pullman, WA. Hereafter, the ssp. inermis will be referred to simply as P. spicata.

Plants of these species were grown from seeds and were vernalized in a cold chamber (5°C) for various lengths of time. The vernalization requirement varied both among and within species. It ranged from 0-4, 0-2, and 2-12 weeks for <u>T. elongatum</u>, <u>P. spicata</u>, and <u>C. violaceum</u>, respectively. Vernalized plants were grown in a greenhouse under long days (18 hours of photoperiod).

Spikes of T. elongatum were emasculated and enclosed in glassine bags before anthesis. Twenty-four hours after hand pollination, a 75 ppm gibber-ellic acid solution was injected into the florets. Half seeds with embryo were aseptically plated on slanted orchid agar medium. Seedlings were transferred into pots at the two leaf stage and maintained in the greenhouse.

Spikes of the F₁ hybrids were fixed in Carnoy's (6:3:1) solution and stored in 70% ethanol. Pollen mother cells (PMCs) were squashed in acetocarmine for meiotic analysis. Mitotic root tip squashes were prepared according to the procedures of Mujeeb-Kazi and Miranda (1985). Karyotype analysis was performed with a microcomputer using the CHROMPAC III¹ software (Green et al. 1984).

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RESULTS

Thinopyrum elongatum X Pseudoroegneria spicata ssp. inermis

Ten caryopses varying in size and color were obtained and cultured from 56 florets pollinated by \underline{P} . $\underline{spicata}$. Three seedlings were obtained but only two were grown to maturity. Both of them are spring type, i.e., they headed in the greenhouse without being vernalized. The hybrid plants were completely sterile. Pollen grains were unstainable with the I_2 -KI solution and anthers were nondehiscent.

The spikes of \underline{T} elongatum \underline{X} \underline{P} spicata had close resemblance to those of \underline{T} . elongatum although some attributes were intermediate to those of both parents (Fig. 1). The spikes of the hybrid resembled \underline{T} elongatum more than \underline{P} spicata in the number of spikelets per spike and in their size and spacing on the axis, but the morphology of its glumes was closest to \underline{P} spicata.

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Meiosis in the hybrids revealed little chromosome pairing (Table 1).

About 7% of the PMCs had 14 univalents at metaphase I (Fig. 2a). Some ring bivalents (Fig. 2b), occasional trivalents (Fig. 2c) and a few hetermorphic bivalents (Fig. 2d) were observed. Up to six bivalents were observed in the hybrids. (Table 1). An average of 1.82 laggards per cell at anaphase I led to 1.67 micronuclei per tetrad.

Mitotic root tip cells showed 14 chromosomes (Fig. 3a) which gave an idiogram matching that constructed from standard idiograms of the parents (Fig. 4a). The S-2 chromosome (Fig. 3a) did not show a small satellite but the pointed short arm indicated the presence of a satellite.

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Thinopyrum elongatum X Critesion violaceum

In the cross <u>T</u>. <u>elongatum</u> X <u>C</u>. <u>violaceum</u>, 23 brown and shriveled seeds were obtained from 46 florets. Only two of them germinated upon culturing and both survived. One of the hybrids is spring type. This hybrid combination was completely sterile with unstainable pollen grains and nondehiscent anthers.

The spikes of this hybrid were intermediate to those of the parents (Fig. 1) for the glume characteristics only. They were shorter than those of both parents and had fewer florets per spike. Being a short plant with narrow leaves, the overall morphology of the hybrids was closer to \underline{C} . $\underline{Violaceum}$ than \underline{T} . $\underline{elongatum}$.

A little less chromosome pairing was observed in the \underline{T} . elongatum X \underline{C} . violaceum hybrid than in the \underline{T} . elongatum \underline{X} \underline{P} . spicata hybrid (Table 1). There was no difference in chromosome pairing between the spring- and winter-type plants. About 16% of its PMCs had 14 univalents at metaphase I (Fig. 5a). Again, ring bivalents (Fig. 5b), trivalents (Fig. 5c)m heteromorphic bivalents (Fig. 5d) and one quadrivalent were observed occasionally. Up to five bivalents were formed at metaphase I (Table 1). Both anaphase-I laggards and micronuclei in tetrads were slightly higher in this hybrid than \underline{T} . elongatum \underline{X} \underline{P} . spicata.

Mitotic cells had 14 chromosomes (Fig. 3b), seven from each parent. The idiogram of the hybrid matched the one developed for a hypothetical hybrid (Fig. 4b), except that the H^V chromosomes were longer than expected. The satellite of J^e4 chromosome was not evident but suggested by the rounded tip of the short arm (Fig. 3b).

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DISCUSSION

Although it is possible, intergeneric hybridization among diploid species in the tribe Triticeae is still difficult. A reasonably high percentage of the pollinated florets, 18 and 50% for T. elongatum X P. spicata and T. elongatum X C. violaceum respectively, set seeds. But not all of hybrid embryos germinated on the culture medium, and some of the hybrids died as young seedlings. Therefore, at the end only a few plants reached maturity. To evaluate the plant-breeding potential of a hybrid combination and its amphidiploids adequately, a larger population of F₁ hybrids is needed. Hundreds or even thousands of florets need to be emasculated and pollinated to obtain the needed hybrids. In an attempt to make diploid hybrids, certain plants of the female parent gave higher numbers of seeds, suggesting the presence of favorable crossability gene(s). Selection and utilization of these desirable plants will make hybridization easier.

However, it may lead to narrower genetic variation for performance

evaluation. Additional research is needed to find a compromise.

Mejotic pairing in the hybrids was higher than expected, yet it was still lower than that expected for interspecific hybrids under the genomic system of classification (Dewey 1984; Löve 1984). Therefore, it is evident that these species have basically different haplomes and belong to different genera. Haploids of T. elongatum had only one rod bivalent (Wang 1985a). It may be assumed that one or two rod bivalent(s) occur in P. spicata and C. violaceum due to autosyndesis. Then, the excess number of bivalents observed in these intergeneric hybrids over the presumed sum of autosyndetic bivalents should be interpreted as allosyndesis or pairing between homoeologous chromosomes of the different haplomes.

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If the average univalent frequency in the diploid hybrids is used as a measurement of phylogenetic distance (Phillips 1966), it can be concluded that the S haplome is closer to H^V than to J^e and that J^e is farther diverged from H^V (Table 1). The same conclusion is reached if a nuclear membrane map is constructed by the distance coefficient method (Jackson 1982).

With the standard idiograms developed for most of the perennial diploid species in the tribe Triticeae (Hsiao et al. 1986), it is now possible to construct an idiogram for a hypothetical intergeneric hybrid and then compare it with one from the actual synthetic hybrids. This study demonstrates that the technique is useful for early identification of putative intergeneric hybrids. Chromosome banding with stains would be required to identify interspecific hybrids because of the intrageneric similarity of karyotypes.

The hybrids reported here, T. elongatum X P. spicata ssp. inermis and T.

elongatum X C. violaceum, have the JeS and JeHV genomic formulas, respectively. The genomic combination EJS(=JeJS) was proposed for Elytrigia (Löve 1984), but genome analysis involving diploid species was not carried out to verify it. Therefore, the two hybrids in this study represent new synthetic genomic combinations. A cross of \underline{T} . elongatum X \underline{P} . stipifolia (Czern. ex Nevski) \hat{A} . Löve \hat{I} , also a JeS combination, gave rise to four seedlings, but all died as seedlings (Wang unpublished). Therefore, genotypic balance determines the survival and failure of plants having a given genomic combination.

Since the F_1 hybrids of these two crosses are relatively vigorous plants, the amphidiploids of these hybrids may be worth evaluating for use as new forage crops. Even if the amphidiploids cannot be used directly, the

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J^eJ^eSS plants would be useful for genome analysis of <u>Elytrigia</u> species.

In addition, they can be backcrossed to the parental species to develop addition, substitution, and translocation lines for facilitating gene flow between genera. Because <u>T. bessarabicum</u> also has the J haplome and many species have S or H haplome, a large number of hybrids involving different species should be synthesized for a fair evaluation of the JS and JH genome combinations.

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1	1	RR-C (1984) Intergeneric and interspecific hybridization among
2		perennial diploid species of the Triticeae tribe in greenhouse. Agron
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4	Wang	RR-C (1984b) Intergeneric and interspecific hybridization among
5		perennial diploid species of the Triticeae tribe in greenhouse. Agron Abst pp 94.
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7	Wang	RR-C (1985a) Monoploid of Thinopyrum elongatum derived from intergeneric
8		hybridization with Agropyron mongolicum. First Can Congr Biol Abst
9		GS2.2.
10	Wang	RR-C (1985b) Genome analysis of $\underline{\text{Thinopyrum}}$ $\underline{\text{bessarabicum}}$ and $\underline{\text{T}}$.
11		elongatum. Can J Genet Cytol (In press).
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14		violaceum X <u>Psathyrostachys</u> <u>juncea</u> . Crop Sci (In press).
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Table 1. Meiotic behavior in Thinopyrum elongatum, Pseudoroegneria spicata ssp. $\underline{inermis}$, $\underline{Critesion}$ $\underline{violaceum}$, and their F_1 hybrids (range is given in the parentheses).

					Metaph	ase I				
Species and hybrids	Genome	2n	No. cells	I	ring II	rod 1	Total		And the second s	Tetrad nn/ceTl
T. elongatum ^a	JJ	14	102	-	6.72 (5-7)	0.28 (0-2)	7.00 (7)	-	0.00	0.03 (0-2)
P. spicata ssp. inermis	SS	14	153	-	6.48 (4-7)	0.52 (0-3)	7.00 (7)	-	0.02 (0-1)	0.01 (0-1)
C. violaceumb	НН	14	102	0.43 (0-6)	5.25 (3-7)	1.53 (0-4)	6.78 (4-7)	-	0.25 (0-3)	0.29 (0-3)
T. elongatum X P. spicata	JS	14	204	9.13 (2-14)	0.08 (0-2)	2.27 (0-6)	2.35 (0-6)	0.05 (0-1)	1.82	1.67 (0-6)
Belongatum X.C. violaceum ^C	Tunt	In	206°	10.07	0.13	1.73	1.86	0.06	2.63 (0-10) CUM	2.46 tation
P. spicata X C. violaceum ^d	SH	14	467	7.12 (0-14)	0.32 (0-3)	2.87 (0-7)	3.19 (0-7)	0.14 (0-3)	0.74 (0-3)	0.41 (0-3)

a Wang (1985b)
b Wang (1984a)
c Also had 0.01 quadrivalent
d Wang et al. (unpublished); also had 0.02 quadrivalent and 0.02 pentavalent.

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Fig. 1.	Spikes of the parents and hybrids, (1 to r): Thinopyrum elongatum,
	T. elongatum X Pseudoroegneria spicata ssp. inermis, P. spicata ssp.
	inermis, T. elongatum, T. elongatum X Critesion violaceum, and \underline{C} .
	violaceum.
Fig. 2.	Meiotic metaphase-I cells of the Thinopyrum elongatum X
	Pseudoroegneria spicata ssp. inermis hybrid. a. Fourteen
	univalents. b. Twelve univalents and one ring bivalent. c.
	Eleven univalents and one trivalent. d. Five univalents, three
	bivalents, and one trivalent; one heteromorphic bivalent is
	indicated by the arrow.
Fig. 3.	Mitotic chromosomes of the hybrids Thinopyrum elongatum X
	Pseudoroegneria spicata ssp. inermis (a) and T. elongatum X
ed by	Critesion violaceum (b). Each chromosome is identified by its haplome symbol and number as in Fig. 4, except that Je and HV
	are abbreviated as J and H, respectively.
Fig. 4.	Idiograms of the hybrids Thinopyrum elongatum X Pseudoroegneria
	spicata ssp. inermis (a) and T. elongatum X Critesion violaceum (b)
	compared to those constructed for hypothetical hybrids based on the
	standard idiograms of the parental species.
Fig. 5.	Meiotic metaphase-I cells of the Thinopyrum elongatum X Critesion
	violaceum hybrid. a. Fourteen univalents. b. Ten univalents, one
	ring and one rod bivalent. c. Seven univalents, two rod bivalents,
	and one trivalent. d. Ten univalents, one ring bivalent, and one
	heteromorphic bivalent (arrowed).

Conspektus of the Triticeae

ASKELL LOVE

Summary

This is a taxonomical and nomenclatural survey of the more than 500 biological taxa of the Triticeae tribe of grasses in a system of thirty-seven genomically defined genera based on twenty-three single-haplome taxa as recently validated elsewhere. An analytical key is given to the genera, which are concisely described and defined; brief information on their genomic constitution is added. When appropriate, subgeneric divisions are described and listed with their synonyms. So are also the accepted names of the biological species and subspecies, with validations of transfers or new names when pertinent; chromosome numbers are added when known, those confirmed by the author with an exclamation mark.

Zusammenfassung

Eine taxonomische und nomenklatorische Übersicht über mehr als 500 zur Tribus Triticeae der Gräser gehörenden biologischen Taxa wird vorgelegt, angeordnet in einem System von 37 Gattungen, die auf 23 einfach-haplomen Taxa, an anderen Stellen neulich gültig gemacht, basieren. Ein analytischer Schlüssel wird für die Gattungen aufgestellt. Diese sind kurz beschrieben und typisiert, und eine zusammenfassende Information über deren genomische Natur ist beigefügt. Wenn zweckmäßig sind die Untergattungen beschrieben und deren Synonyme zusammengestellt worden. Auch die gultigen Namen von biologischen Arten und Unterarten sind mit Synonymen sowie mit Beschreibungen, neuen Kombinationen oder neuen Namen versehen, wenn erforderlich. Die Chromosomenzahlen sind beigefügt, soweit diese bekannt sind; solche, die vom Verfasser bestätigt werden konnten, sind durch ein Ausrufungszeichen gekennzeichnet.

Introduction €

This report is intended as a comprehensive survey of the 500-odd species and subspecies of the wheatgrasses in a system of thirty-seven genomically defined genera pased on twenty-three single-haplome taxa, as recently advocated by the author (A. Löve, 1982: Generic evolution of the wheatgrasses. Biologisches Zentralblatt 101: 199-212). The genera, which are distinguished by clear morphological traits, are essentially incompatible or display a very low crossability owing to considerable repatterning of their chromosome complements beyond the limit of homeologous pairing, although they, nevertheless, seem to manifest a differentiation of a single original chromosome set. Fifteen of the genera have not evolved beyond their monotypic original haplome and are geographically restricted, whereas others have either differentiated into few to many distinct species, or united to form alloploid genera that in turn have produced a considerable array of species and subspecies, which have invaded most grasslands in the arctic and temperate regions of the world. In such a genetical system, species need to be biologically defined by their reproductive isolation caused by linear or numerical chromosome rearrangements within the limits of some

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\$456: for Elynn throddinaus plant: Elynn throddians

p459. Silling: Live, rod A. Line

g 468. for Elymo lagraphy of ming dulle, mar line It fire parts to the ofte Ju. Ap. litimais adds 2 men

ized by Huntulnstitute for Botanical Documentation

a SII: 16th Lac. Iron, rent: Iron + DMM.

28thaling. 1.445, 465, 473, 482, 501 mg.

Because of distance the set groß in sent carfely by the nature you with little by for the author they except a for request here coupling the most distance are being;

For recons legal the cutod of the state author of extrary, groups had to be largelish by the that is the corporate by the party own in the agent of a whole to for many engine where extrary property from stopped by the following great of the following most extrary.

p. 447, line 30 11 ming: 2 m2.

p. 443; the 20 to many control of the control of th Espis protector, retroferen e elle. There in forty while a Texan 4 (1935) in An Byon LXXXVII

p. 4 56, line 13, sell k, Elynn thorothing (olan) 6. Engl. Tre- 32.640

p. 448, bu 26 n may: 2 m= 28

p. 473, tie 5, should be: Elyon termiles "A. Live (also :- Index, p. 514)

p. 365, lives 36 = 53, the market in; E. elympeter soties (Region) heavy

p. 468, him 23 is many , 2 m2 ...

p. 471, be 32, and Ahroppe. J. Agr. prom

go 492, has to the making 20 ct) half one lot in 33 fet opening, it 2-028 in his 20 state in 2-1 86.

p. 501, bu 25, adds or DMM.