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THE INHERITANCE OF RESISTANCE TO POWDERY MILDEW IN INTERSPECIFIC HYBRIDS AND INDUCED AMPHIPLOIDS OF *ZINNIA ELEGANS* JACQ. AND *Z. ANGUSTIFOLIA* HBK[1]

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SUMMARY

Sterile interspecific hybrids and colchicine-induced amphiploids of *Zinnia elegans* JACQ. and *Z. angustifolia* HBK were examined to determine the mode of inheritance of resistance to *Erysiphe cichoracearum* DC ex MERAT. Fertility was restored through colchicine treatment of two sterile hybrids of species reciprocal parentage which differed in ray petal response to the pathogen. Derived amphiploids were subsequently intercrossed to overcome the lack of segregation for this trait due to genetic control of pairing upon chromosome doubling. Resistance to *E. cichoracearum* appears to be complexly inherited in both leaves and ray florets of sterile hybrids and induced amphiploids. Two major dominant genes have been implicated in conferring resistance in ray petal tissue of derived amphiploids. Data obtained from the F_1 hybrid progeny of the intercrossed amphiploids indicate that this trait is not cytoplasmically inherited. It is speculated that the genes conferring resistance in the ray florets are acting independently from those controlling leaf resistance and that most, if not all, of the resistance genes are inherited from *Z. angustifolia*.

INTRODUCTION

Powdery mildew, caused by *Erysiphe cichoracearum* DC ex MERAT, is the most important disease of *Zinnia elegans* JACQ. in most areas of commercial production. Severe epiphytotics on this popular garden ornamental have caused considerable reductions in seed sales in recent years (DREWLOW, personal communication).

Attempts to hybridize *Z. elegans* ($2n = 24$) (TORRES, 1963; RAMALINGAM et al., 1971; TERRY-LEWANDOWSKI et al., 1984) with the highly resistant species, *Z. angustifolia* HBK ($2n = 22$) (MENON et al., 1969; RAMALINGAM et al., 1971; TERRY-LEWANDOWSKI et al., 1984) have not been uniformly successful (ANDERSEN, 1971; RAMALINGAM et al., 1971; BOYLE & STIMART, 1982). The primary limitations appear to be interspecific cross incompatibility and F_1 hybrid sterility. BOYLE & STIMART (1982)

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successfully recovered a limited number of hybrids from reciprocal matings and restored fertility in the F_1 by treatment of axillary buds with colchicine. Subsequent cytological examination in this laboratory of F_1 hybrids ($2n = 23$) and colchicine-induced amphiploids ($2n = 46$) revealed partial genome homology in the F_1 but strict bivalent pairing upon somatic doubling due to preferential association of homologous chromosomes (TERRY-LEWANDOWSKI et al., 1984). Consequently, the amphiploids behaved cytologically and genetically as fully homozygous diploids and failed to segregate in subsequent generations. These conclusions were further substantiated by the lack of segregation for resistance to *E. cichoracearum* following greenhouse and field inoculations (TERRY-LEWANDOWSKI & STIMART, 1983) and for morphological traits among amphiploid families (TERRY-LEWANDOWSKI et al., 1984). It was demonstrated that non-segregating amphiploids of *Z. angustifolia* × *Z. elegans* 'Cherry Ruffles' were completely resistant to powdery mildew on both leaves and ray florets, whereas amphiploids of *Z. elegans* 'Whirligig' × *Z. angustifolia* exhibited resistance on the foliage but susceptibility on senescing ray florets (TERRY-LEWANDOWSKI & STIMART, 1983).

The purpose of this investigation was to determine the mode of inheritance of resistance to *E. cichoracearum* in interspecific hybrids and induced amphiploids of *Z. elegans* and *Z. angustifolia.*

MATERIALS AND METHODS

Sterile F_1 hybrids of *Z. elegans* and *Z. angustifolia* were asexually propagated from stem tip cuttings treated with Hormodin 2 (0.3% indolebutyric acid) from stock plants maintained at the University of Maryland (BOYLE & STIMART, 1982). Fertile amphiploids of *Z. angustifolia* × *Z. elegans* 'Cherry Ruffles' (C_2-CR) and *Z. elegans* 'Whirligig' × *Z. angustifolia* (C_2-W) were generated through colchicine treatment of axillary buds as previously described (TERRY-LEWANDOWSKI et al., 1984). All sterile F_1 hybrids and amphiploids were maintained in the greenhouse and fertilized weekly for the duration of the experiments.

Twenty-one sterile F_1 hybrids were evaluated for resistance to *E. cichoracearum* in a completely random experimental design with four replications per hybrid; the study was replicated in time over two winters. Inoculations were performed by shaking heavily infected *Z. elegans* plants above flowering test plants at 3-day intervals for 12 days. Plants were rated as resistant (R) or susceptible (S) on leaves and ray florets two weeks after the first inoculations were made.

C_2–CR (resistant) and C_2-W (susceptible) amphiploids were crossed reciprocally to induce segregation and to determine whether resistance in the ray florets was controlled by cytoplasmic or nuclear effects. Hybrid progeny were designated as F_1'–CR (C_2–CR × C_2–W) and F_1'–W (C_2–W × C_2–CR) (Fig. 1). Control plants were produced by self-pollination of the parental amphiploids and designated as C_3-CR and C_3-W, respectively. All pollinations were performed by hand under fabric tents (24% light reduction) to prevent contamination with foreign pollen. Controls and F_1' hybrids were arranged in a randomized complete block design with 30 plants per genotype replicated over five blocks. Artificial inoculations with *E. cichoracearum* were performed as previously described (TERRY-LEWANDOWSKI et al., 1984). Disease severity on ray florets was evaluated according to the following scale: resistant = no macro-

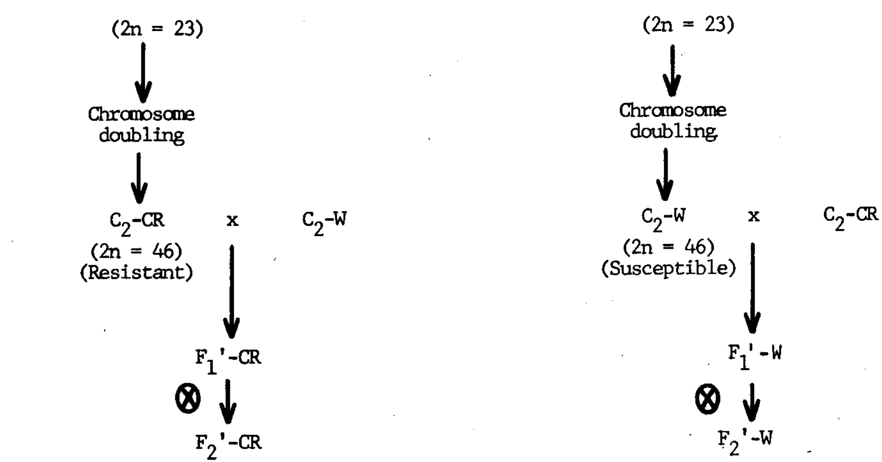

Fig. 1. Pedigree of intercrossed amphiploids of *Zinnia elegans* and *Z. angustifolia* for induced segregation of resistance to *Erysiphe cichoracearum* in ray florets.

scopically visible colonies; moderately susceptible = few colonies with sparse, nonsporulating mycelium; and susceptible = host tissue heavily infected with nonsporulating mycelium.

Ten F_1 hybrids of each cross were randomly selected to serve as parents for F_2' families (Fig. 1). The progeny arising from self-pollination were evaluated in a completely random design with 472 plants in the C_2'–CR and 445 in the C_2'–W populations. Individual plants were scored as either resistant (no macroscopically visible colonies) or susceptible (host tissue infected with non-sporulating mycelium) on senescing ray petal tissue. Data from the F_1' and F_2' populations were analysed using a Chi-square goodness of fit test.

RESULTS

The sterile F_1 hybrids of *Z. angustifolia* and *Z. elegans* exhibited a differential response to *E. cichoracearum* on leaves and ray florets. Of the 21 genotypes evaluated, only *Z. angustifolia* × *Z. elegans* 'Cherry Ruffles' displayed complete resistance on both foliar and blossom tissues. The remainder of the F_1 hybrids were susceptible on ray florets and either resistant or susceptible on leaves. Differences in leaf resistance were observed in crosses where a single *Z. elegans* cultivar served as a parent for more than one hybrid offspring.

The F_1'–CR and F_1'–W progeny arising from reciprocal crosses of the colchicine-induced amphiploids C_2–CR and C_2–W were not significantly different from one another with respect to ray petal resistance. Reactions were, however, intermediate and did not resemble those of either parent (Table 1). The selfed C_3–CR control plants deviated slightly from the expected frequency of 100% resistant due to genetic control of pairing, with three plants classified as moderately susceptible; this discrepancy is likely due to a misclassification of data. The C_3–W controls behaved as expected with 148 individuals scored as susceptible and only two as moderately susceptible.

Table 1. Reactions to *Erypsiphe cichoracearum* on ray florets of F_1' hybrids derived from crosses of resistant and susceptible amphiploids of *Zinnia elegans* and *Z. angustifolia.*

Plant type	Reaction[a]		
	resistant	moderately susceptible	susceptible
C_3–CR[b]	147	3	0
C_3–W[c]	0	2	148
F_1'–CR[d]	0	145	5
F_1'–W[e]	4	145	1

[a] Based on the disease severity scale: resistant = no macroscopically visible colonies; moderately susceptible = few colonies with sparse, non-sporulating mycelium; and susceptible = ray petal tissue heavily infected with non-sporulating mycelium.

[b] *Z. angustifolia* × *Z. elegans* 'CherryRuffles' (C_3 generation).

[c] *Z. elegans* 'Whirligig' × *Z. angustifolia* (C_3 generation).

[d] C_2–CR × C_2–W.

[e] C_2–W × C_2–CR.

A good fit was obtained for a digenic ratio of 15 resistant: 1 susceptible in both F_2' populations of intercrossed amphiploids (Table 2). Although the classification between resistant and susceptible entries was for the most part unambiguous, differences in disease severity existed among plants rated as susceptible.

DISCUSSION

The results of this investigation suggest multiple gene action for resistance to *E. cichoracearum* in different tissues of sterile F_1 hybrids and colchicine-induced amphiploids of *Z. elegans* and *Z. angustifolia.* It is possible that most, if not all, of the resistance genes operating in leaves and ray florets are inherited from *Z. angustifolia* and are not present in the *Z. elegans* genome because four decades of research with the latter species have repeatedly failed to yield resistant cultivars (DREWLOW, personal communication).

The colchicine-induced amphiploids have previously been demonstrated to behave as fully-homozygous diploids due to genetic control of pairing (TERRY-LEWANDOWSKI

Table 2. Reactions to *Erysiphe cichoracearum* on ray petal tissue of F_2' populations from crosses of resistant and susceptible amphiploids of *Zinnia elegans* and *Z. angustifolia.*

Cross	Reaction of F_2' population[a]		
	resistant	susceptible	P value (15:1)
F_2'–CR[b]	438	34	0.50–0.75
F_2'–W[c]	415	30	0.25–0.50

[a] Based on the disease severity scale: resistant = no macroscopically visible colonies and susceptible = ray petal tissue infected with non-sporulating mycelium.

[b] (*Z. angustifolia* × *Z. elegans* 'Cherry Ruffles') × (*Z. elegans* 'Whirligig' × *Z. angustifolia*).

[c] (*Z. elegans* 'Whirligig' × *Z. angustifolia*) × (*Z. angustifolia* × *Z. elegans* 'Cherry Ruffles').

et al., 1984). Intercrossing these segmental allopolyploids served to induce chromosomal associations and segregation for resistance to *E. cichoracearum*. The genetic analysis of the F_2' progeny suggests the presence of two major dominant genes operating in the ray florets of induced amphiploids. Furthermore, the absence of phenotypic differences in the F_1' progeny of reciprocal matings indicates that these genes are located in the nucleus and are therefore not cytoplasmically inherited.

Further investigation is suggested to determine the mode of inheritance of foliar resistance to *E. cichoracearum* in interspecific hybrids and induced amphiploids of *Z. elegans* and *Z. angustifolia*. The experimental procedures should parallel those of the present study to induce genetic and phenotypic segregation in segmental allopolyploids which exhibit a differential response to the pathogen. In addition, progeny of the F_3' generation should be evaluated to confirm the observed segregation ratios for resistance in the ray florets. It is anticipated that the information drawn from these investigations will lend further definition to the proposed interactions of nuclear genes conferring resistance to *E. cichoracearum* in different plant tissues of induced amphiploids.

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