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The function of pollen tetrads in *Typha (Typhaceae)*

Funktion von Pollen-Tetraden bei *Typha (Typhaceae)*

by

Marc S. NICHOLLS and Christopher D.K. COOK

1. INTRODUCTION

The dispersal of pollen and the efficiency of pollination in Typha has been studied by Krattinger (1975, 1978). Typha is wind pollinated but is unusual in that in some species the pollen is dispersed in tetrads. Taking the list of plants by ERDTMAN (1945) as a basis it is found that tetrads occur in about 44 families and 1030 genera of angiosperms. Their adaptive significance is unclear, but they are mostly found in insect pollinated genera (1015 genera = 98.5%). Of the rest, two are pollinated in or on water (Elodea and Halophila) and 13 (1.3%) are wind pollinated. The relative scarcity of tetrads among wind pollinated plants suggests that their development is not part of the wind pollination syndrome. In fact, POHL (1929) felt that only explanation of wind pollinated plants with tetrads was that they had evolved from insect pollinated ancestors.

For Myrothamnus (Myrothamnaceae), Richea (Epacridaceae) and perhaps also the nine genera of the Juncaceae, POHL's explanation is convincing, also Scheuchzeria (Scheuchzeriaceae) which has its pollen in dyads probably had entomophilous ancestors. The remaining wind pollinated genus with tetrads is Typha and even POHL was unable to suggest any insect-pollinated progenitors.

The tetrads of Typha latifolia L. have the longest axis 30-55 µm, a weight of $5.419 \pm 0.294 \times 10^{-9}$ g, and a terminal velocity of 2.9-4.4 cm/s. According to the limits suggested by POHL (1937 a,b) and repeated in WHITEHEAD (1969), the physical constitution of the tetrads of T. latifolia is about average for a wind pollinated plants. From an aerodynamic point of view, the tetrad pollen of Typha appears to be neither disadvantageous nor particularly advantageous.

Typha angustifolia L. is morphologically and ecologically very similar to T. latifolia but sheds its pollen as single grains. Both species are patristically very close and when crossed in both directions yield fertile hybrids. KRATTINGER (1975, 1978) showed that T. latifolia produces at least twice as many male gamete units (i.e. single pollen grains) in each inflorescence as T. angustifolia.

WILLSON (1979) suggested that for species having more ovules per flower than pollen grains in a dispersal unit, the simultaneous arrival of multi-pollen grain units may be advantageous in effecting fertilization compared with the arrival of an equal number of single grains over a period of time. Almost all wind pollinated plants with tetrad pollen have more than four ovules to each flower, a point clearly made by POHL (1929). However, there are exceptions: Luzula (Juncaceae) has three ovules per flower and Typha has flowers bearing solitary ovules. WILLSON's suggestion has no apparent validity for the tetrad bearing species of Typha.

WILLSON (1979) also predicted that since tetrads lead to heavier losses than single grains when pollination is not effective, the vectors of clumped pollen are likely to be more specific than those of single grains. Probably no vector is less specific than wind, so again Typha is an exception.

Sometimes even logic is not your friend. Typha breaks all these rules by being wind pollinated, having pollen in (expensive) tetrads and having a single ovule per flower. KRATTINGER (1975, 1978) and MÜLLER-DOBLIES and MÜLLER-DOBLIES in HEGI (1977) have claimed that pollen tubes can grow

from the stigma of one flower to another. We felt that this aspect was worth investigating further.

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2. METHODS

Portions of naturally pollinated inflorescences of T. latifolia plants growing in the Botanic Gardens of the University of Zürich were collected at anthesis and fixed in 2.5% glutaraldehyde in cacodylat buffer (0.1 M, pH 7.2). Some portions were examined intact and some after dissection. Samples were observed with a Cambridge S4 scanning electron microscope.

3. RESULTS

The single pollen grains comprising the tetrad of T. latifolia have a reticulate exine with a single aperture. The grains are held in tetrad formation by fine, bridge-like connections shown in Fig. 1a.
Most stigmas examined had several to many tetrads present on the surface (Fig. 1b). Most tetrads were of the square type according the scheme of

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Abb. 1 (S. 115). Typha latifolia: a. Pollen-Tetrade, zwei keimende Pollenkörner (Massstab: 10 µm); b. Pollenschläuche zwischen und über Narben wachsend (Massstab: 200 µm); c. Pollenschläuche beim Ueberqueren einer bestäubten Narbe zu einer unbestäubten Narbe (Massstab: 100 µm); d. wie bei c. Massstab: 200 µm).

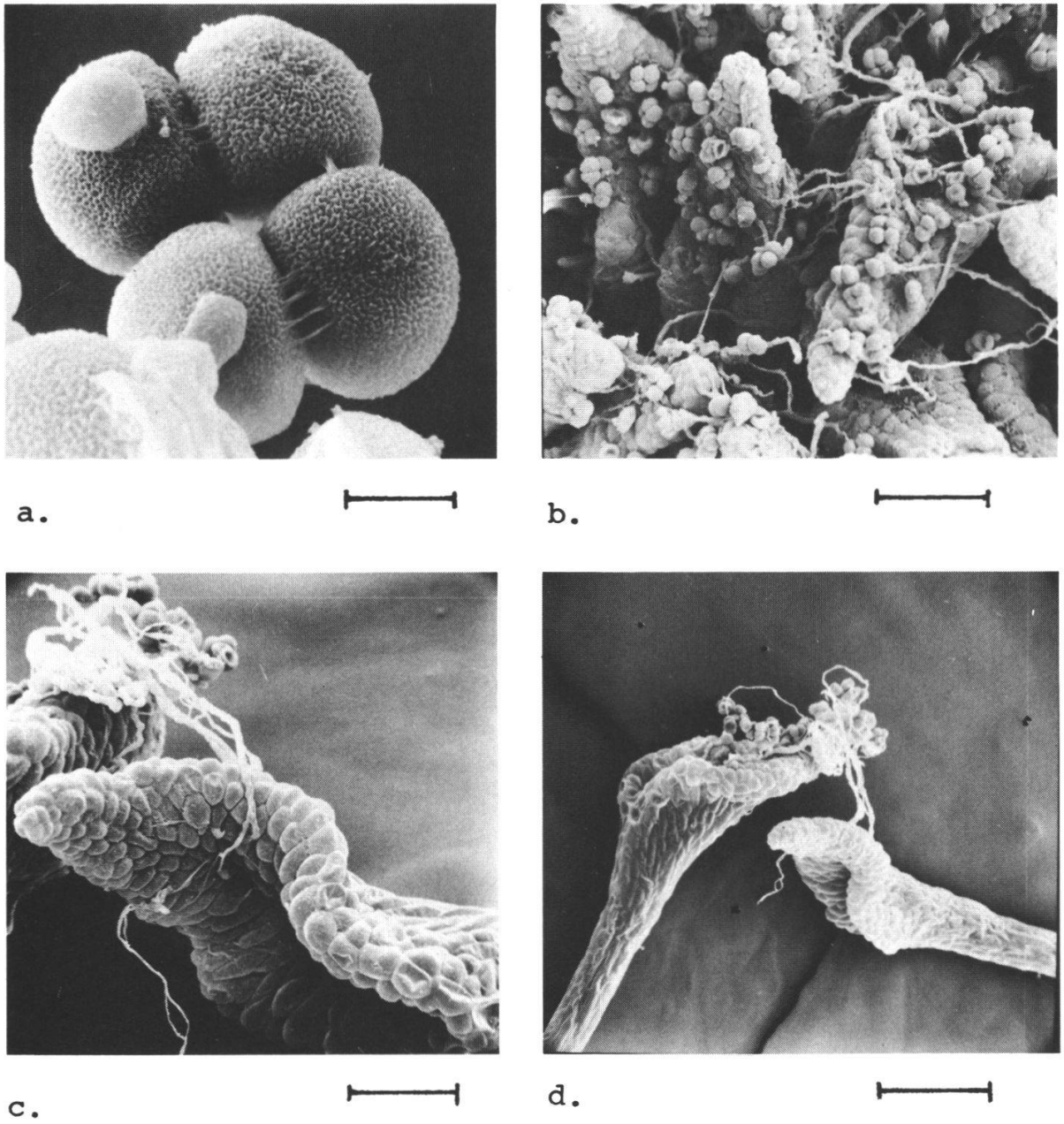

Fig. 1. Typha latifolia: a. pollen tetrad, two grains germinating (scale bar: 10 µm); b. pollen tubes growing over and between stigmas (scale bar: 200 µm); c. pollen tubes crossing from pollinated stigma to unpollinated stigma (scale bar: 100 µm); d. as for c. (scale bar: 200 µm).

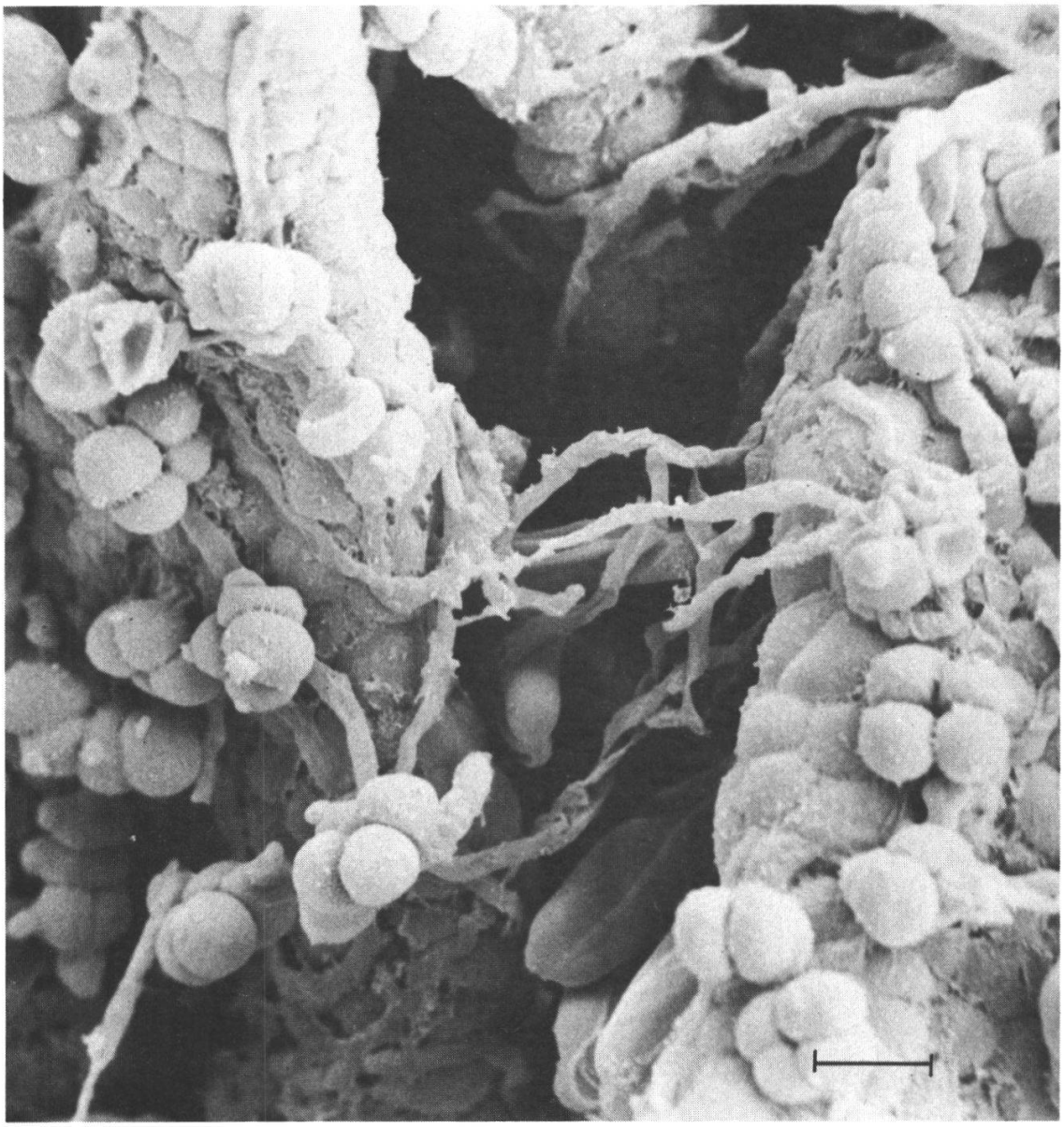

Fig. 2. Typha latifolia: pollen tetrads on naturally pollinated stigmas showing pollen tubes growing from stigma of one flower to the stigma of another (scale bar: 50 µm).

Abb. 2. Thypha latifolia: Pollen-Tetraden auf natürlich bestäubten Narben. Pollenschläuche wachsen von der Narbe einer Blüte auf die Narbe einer anderen Blüte. (Massstab 50 µm).

ERDTMAN (1945), confirming studies by KRATTINGER (1978) who showed 81% of T. latifolia tetrads to be of this type.
Pollen tubes germinate from the two sets of more-or-less circular pori shown in Fig. 1a. Initial germination presumably occurs on that face of the tetrad having contact with the stigmatic surface, though in many cases two or three pollen tubes appear to have germinated virtually simultaneously and without all having obvious stigmatic contact.
After germination, the pollen tubes grow rapidly over the stigma and frequently traverse from the stigma of one flower to that of another. This results in the characteristic mass of intertwining pollen tubes shown in Fig. 1b and Fig. 2. Our observations suggest that pollen tubes germinating on one stigma may even grow down the stigma of a neighbouring flower, thereby effecting fertilization (Fig. 1c and d).

4. DISCUSSION

Despite the predictions of WHITEHEAD (1969), WILLSON (1979) and others, the central question posed by T. latifolia is why should a species having a single ovule per flower have pollen dispersed in units of four?

WILLSON (1979) predicted that tetrads will lead to heavier losses than single grains when pollen vectors are not specific. In the case of T. latifolia we turn this hypothesis on its head and claim that conversely, when pollination is effective, having pollen grains in tetrads will result in a threefold increase in the number of male gametes transferred per effective pollination.
The grains of the tetrad of T. latifolia seem to behave quite independently on the stigma and may feasibly fertilize four separate flowers. Comparing the percentage pollination (pollen on the stigma) and fertilization (number of seeds) in T. angustifolia (single grains) and T. latifolia (tetrads), KRATTINGER (1975,1978) found that in the middle of the inflorescence, 58% of the stigmas of T. angustifolia had pollen grains but the final seed set was 37%. In T. latifolia, 31% of the stigmas had tetrads but 67% of flowers set seed. According to these data, single grains resulted in 0.6 fertilizations/pollination whereas tetrads yield-

ed 2.2 fertilizations/pollination. Obviously then, one tetrad is capable of fertilizing more than one flower.

Despite the increased cost to T. latifolia in producing over twice as many male gamete units (single pollen grains) per inflorescence, we propose that this is more than offset by an increase in fertilization/pollination of over three times that of the related single grain species T. angustifolia. Further experimental studies of similar situations are required to fully elucidate the function of tetrads as a unit of pollen dispersal.

SUMMARY

Typha latifolia L. is wind pollinated, has a single ovule per flower and has pollen in tetrads. This contradicts all previous theoretical predictions regarding the function of pollen tetrads as units of dispersal. The closely related species T. angustifolia L. is similar but has its pollen grains in single units. We compare the benefits and handicaps of each and show that while T. latifolia produces over twice as many male gamete units as T. angustfolia, the tetrad formation of the former results in an increase of more than threefold in the efficiency of the gametes in effecting fertilization. Pollen tubes are capable of traversing from the stigma of one flower to another and effecting fertilization of neighbouring flowers.

ZUSAMMENFASSUNG

Typha latifolia L. ist windbestäubt, hat eine einzige Samenanlage je Blüte und Pollenkörner in Tetraden. Dies widerspricht allen bisherigen theoretischen Voraussagen über die Funktion von Pollen-Tetraden als Bestäubungseinheiten. Die nah verwandte Art T. angustifolia L. ist ähnlich, sie hat aber einzelne Pollenkörner. Wir vergleichen die Vor- und Nachteile von Tetraden und einzelnen Pollenkörnern in Typha und zeigen, während T. latifolia zweimal mehr männliche Gameten erzeugt als T. angustifolia, dass die Tetraden der ersten Art eine mehr als dreifache Zunahme in der Effizienz der Gameten in der Befruchtung hat. Pollenschläuche sind fähig von der Narbe einer Blüte auf die Narbe einer anderen hinüberzuwachsen und dadurch Nachbarblüten zu befruchten.

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