

HYBRIDS BETWEEN DUTCH TORMENTILLAE (POTENTILLA, ROSACEAE)

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SUMMARY

Hybridization in Dutch populations of *Potentilla anglica*, *P. erecta* and *P. reptans* was investigated. Chromosome counts were carried out for 342 plants collected from 40 populations. The chromosome number $2n = 56$ was established for 52 plants all belonging to *P. anglica*, while 225 plants were found to possess $2n = 28$. Of these 117 were identified as *P. erecta* and 108 as *P. reptans*. The number of $2n = 42$ was counted for 50 specimens which belonged all, except 6 *P. × mixta* plants, to *P. × suberecta*. In 15 counts intermediate chromosome numbers were ascertained between $2n = 28$ and $2n = 42$, and between $2n = 42$ and $2n = 56$, which most probably were due to back crossing of *P. × suberecta* with one of the parental species. *P. × suberecta* was found in 13 populations and *P. × mixta* in only two. The hybrid *P. erecta × reptans* was not met with. Detailed study of some *P. × suberecta* populations revealed that this hybrid always grew mixed up with *P. erecta*, often in large quantities. In morphological characters and ecological amplitude it ranged from *P. erecta* to *P. anglica*. Its pollen and fruit fertility was c. 1/3 respectively c. 2/3 of that of the parental species. The functioning of the pollen was investigated in five *P. erecta* populations. Transport of pollen was found to occur by wind, but chiefly by insects from the families: Syrphidae, Muscidae, Tachinidae, Chloropidae and Thripidae. Artificial cross fertilisation yielded more mature seeds than id. self fertilisation, while apogamy was not demonstrated. Finally, literature data and own observations were combined in a hybridization scheme.

1. INTRODUCTION

The genus *Potentilla* comprises about 400 species, mainly distributed in the temperate and arctic regions of the northern hemisphere. The basic chromosome number in the genus is $X = 7$. Most species are polyploids and tetra-, hexa- and octoploids are common, but higher ploidy levels are also found, e.g. $2n = 112$ in the Mexican *Potentilla haematochroa* (see FEDEROV 1969). Diploids are usually amphimictic and allogamous, polyploids are often pseudogamic agamosperms. Vegetative reproduction is known for many species.

Within the genus hybridization is an important phenomenon, not only at diploid level, but also at higher ploidy levels. The latter is possible because pseudogamic species are sometimes able to reproduce sexually as well (HUNZIKER 1954; RUTISHAUSER 1948). In this way intricate polyploid complexes have arisen.

Our knowledge of the reproduction in *Potentilla* is far from complete, because relatively few species have been thoroughly investigated up to now. Most species studied turned out to be principally pseudogamous agamosperms and they re-

present polyploid complexes e.g. *P. argentea*, *P. cinerea*, *P. crantzii*, *P. tabernaemontani*. (ACHARYA GOSWAMI & MATFIELD 1974; ASKER 1976, 1977; CZAPIK 1962a, b, c; HUNZIKER 1954; MÜNTZING 1958a-d; RUTISHAUSER 1943, 1945, 1948, 1949; RUTISHAUSER & HUNZIKER 1954).

The group Tormentillae as described by WOLF (1908), comprises eight species of which three are found in Europe: *P. anglica*, *P. erecta* and *P. reptans*. These three species stand close together even in such a way that *P. anglica* is suggested to be an allo-octoploid ($2n=56$) which originated by hybridization of the two other species, *P. erecta* and *P. reptans* (STOMPS 1951). This opinion was later confirmed by MATFIELD & ELLIS (1972). According to SCHWENDENER (1970), *P. erecta* and *P. reptans* should be considered to be allo-tetraploids. The three species are amphimictic but a tendency towards apospory is present (SCHWENDENER 1970). Vegetative reproduction by means of runners is, in particular, important in *P. reptans* but it may also occur in *P. anglica*. Hybrids between the three species are known from wild populations (BALL et al. 1968; BRÜKŠS 1930; MATFIELD 1966, 1972) as well as a result of crossing experiments (CZAPIK 1969; MATFIELD & ELLIS 1972; MATFIELD et al. 1970; SCHWENDENER 1970).

Morphological variation is comparatively slight in *P. reptans*, moderate in *P. erecta* and *P. anglica*, and fairly large in their hybrids. In table 1, the morphological characters, of the three species mentioned and their hybrids, as given in the literature, are summarized.

The present paper gives data on morphology, ecology, cytology and reproduction of *P. anglica*, *P. erecta* and *P. reptans* and the hybrids *P. × suberecta*. (*P. anglica* × *erecta*) and *P. × mixta* (*P. anglica* × *reptans*).

2. MATERIAL AND METHODS

Plants used in this study were dug out in the field from 40 populations (see fig. 1) and transplanted to the experimental garden.

Morphological data were obtained from voucher specimens collected in the field and in the experimental garden as well as from living material that originated from nature and the experimental garden.

Chromosome counts were made on metaphase plates of roottip mitosis. For this purpose the root tips were fixed in Carnoy or in Karpechenko's fixative. The first were stained with orcein and squashed, the latter were embedded in paraffin wax, sectioned at 15 micron and stained according to Heidenhain's haematoxylin method. Observations on reproduction were made by counting well-developed fruits. Pollen fertility was studied with the aid of cotton-blue lactophenol. Artificial pollination experiments were carried out both in the field and in the experimental garden. Flower buds of plants growing in the field were enveloped with fine nylon curtain (mesh width 0.8 mm) in a double layer.

Table 1. Discriminating characters of *P. erecta*, *P. anglica*, *P. reptans* and their hybrids as abstracted from the literature. Data for *P. erecta* × *reptans* based on a single, artificially obtained specimen (MATFIELD 1972).

| | <i>P. erecta</i> (syn. <i>P. tormentilla</i>) | <i>P. anglica</i> (syn. <i>P. procumbens</i>) | <i>P. reptans</i> | <i>P. × suberecta</i> = <i>P. anglica</i> × <i>erecta</i> | <i>P. × mixta</i> (syn. <i>P. × italica</i>) = <i>P. anglica</i> × <i>reptans</i> | <i>P. erecta</i> × <i>reptans</i> |
|--|---|--|--|--|--|--|
| stems | 10–50 cm long; procumbent to suberect; when at flower much dichotomously branched | 10–80 cm long; procumbent; when at flower dichotomously branched | often > 100 cm long; procumbent; sparsely branched | 10–70 cm long; procumbent; when at flower dichotomously branched | 20–200 cm long; procumbent; sparsely branched | c. 8 cm long; procumbent; branched |
| roots at nodes (rate of vegetative reproduction) | not present | in late summer and autumn present | well developed | not present | present | not present |
| radicle leaves | leaflets 3(–5) | leaflets 3–5 | leaflets 5–7 | leaflets 3(–5) | 70–90% with 5, 10–30% with 3–4 leaflets | leaflets (3–)5 |
| cauline leaves | (sub)sessile; leaflets 3(–5) | more (lower) or less (upper) petiolate; leaflets (1–) 3–5 | long petiolate; leaflets (3–) 5 (–7) | short petiolate; leaflets 3(–5) | (short) petiolate; 70–90% with 5, 10–30% with 3–4 leaflets | short petiolate to sessile; leaflets 3(–5) |
| stipules | usually tri- to pentafid or -partite | entire to trifid | usually entire | bi- to tetrafid | entire to trifid | entire to trifid |
| flowers | Ø (6–)10(–15) mm four-merous | Ø (10–)15–18 mm; four- (five-) merous | Ø 18–25 mm; five-merous | Ø 7–17 mm; four- (five-) merous | Ø 14–22 mm; four- or five-merous | Ø 13–15 mm; four- or five-merous |
| number of carpels | 4–8 (–20) | 20–40 (–50) | 60–120 | 10–30 | 20–75 | c. 25 |
| % stainable pollen (rate of pollen fertility) | high | 30–90% | high | 0–60% | 0–10% | c. 12% |
| % well developed fruits | high | ? | high | < 15% | < 1% | < 1% |



Fig. 1. *Potentilla* populations investigated: 1 Gulpen; 2 Westenschouwen; 3, 4, 5 Voorne; 6 Kijkduin; 7 Streefkerk; 8 Reeuwijk; 9 Nieuwkoop; 10 Bergambacht; 11 Schoonhoven; 12, 13 Lopik; 14 Benschop; 15 IJsselstein; 16 Nieuwegein; 17 Vianen; 18 Enspijk; 19, 20 Culemborg; 21 Beusichem; 22 Botshol; 23 Loenen; 24 Maartensdijk; 25 Lage Vuursche; 26 Hilversum; 27 Bilthoven; 28 Soestdijk; 29 Rhenen; 30 Doornenburg; 31 Speulde; 32 Staverden; 33, 34 Ilperveld; 35 Egmond; 36 Schoorl; 37 Hondsbossche Zeewering; 38, 39, 40 Schiermonnikoog.

3. RESULTS

3.1. Cytology

The chromosome number of 342 plants was determined: 225 plants had the tetraploid number $2n=28$, 50 the hexaploid number $2n=42$, and 52 the octoploid number $2n=56$. Five plants had a chromosome number between $2n=28$ and $2n=42$, and 10 between $2n=42$ and $2n=56$ (see fig. 2).

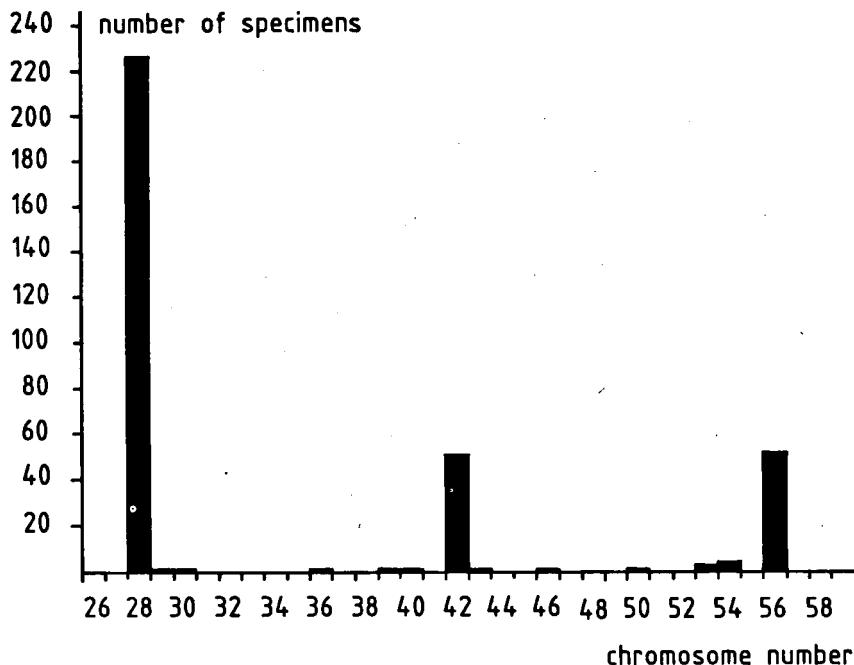


Fig. 2. Chromosome numbers found in 342 *Tormentillae* plants from 40 populations.

Of the 225 tetraploid plants 108 were identified as *P. reptans* and 117 as *P. erecta*. Of the 50 hexaploid plants 44 belonged to *P. × suberecta* and the other 6 to *P. × mixta*. The 52 octoploids ($2n=56$) were all identified as *P. anglica*. It seems likely that the intermediates between 28 and 42, and 42 and 56 chromosomes represent backcrossings between *P. × suberecta* and *P. erecta*, and between *P. × suberecta* and *P. anglica*, respectively. Backcrossing of *P. × suberecta* with *P. reptans* could be excluded on the ground of morphological criteria, moreover *P. reptans* was absent in most of the *P. × suberecta* locations. In a few cases aneusomaty was observed in *P. erecta* and *P. reptans* with deviations from 25 to 29 chromosomes. In one plant of *P. anglica* endoploidy with metaphase plates with $2n=112$ chromosomes was encountered.

3.2. Distribution and ecology

In three localities *P. anglica*, *P. erecta* and *P. reptans* and the hybrid *P. × suberecta* were found growing together (Voorne $2\times$ and Streefkerk). The same combination, but without *P. reptans*, was found in eight localities (Reeuwijk, Nieuwkoop, Botshol, Ilperveld $2\times$ and Schiermonnikoog $3\times$). In two populations *P. erecta* and *P. × suberecta* occurred (Speulde and Staverden). *P. × mixta* was found once growing together with *P. reptans* (Bilthoven) and once growing together with *P. anglica* (Lage Vuursche). The combination *P. erecta* and *P. reptans* was found once in the vicinity of Egmond. On all other locations

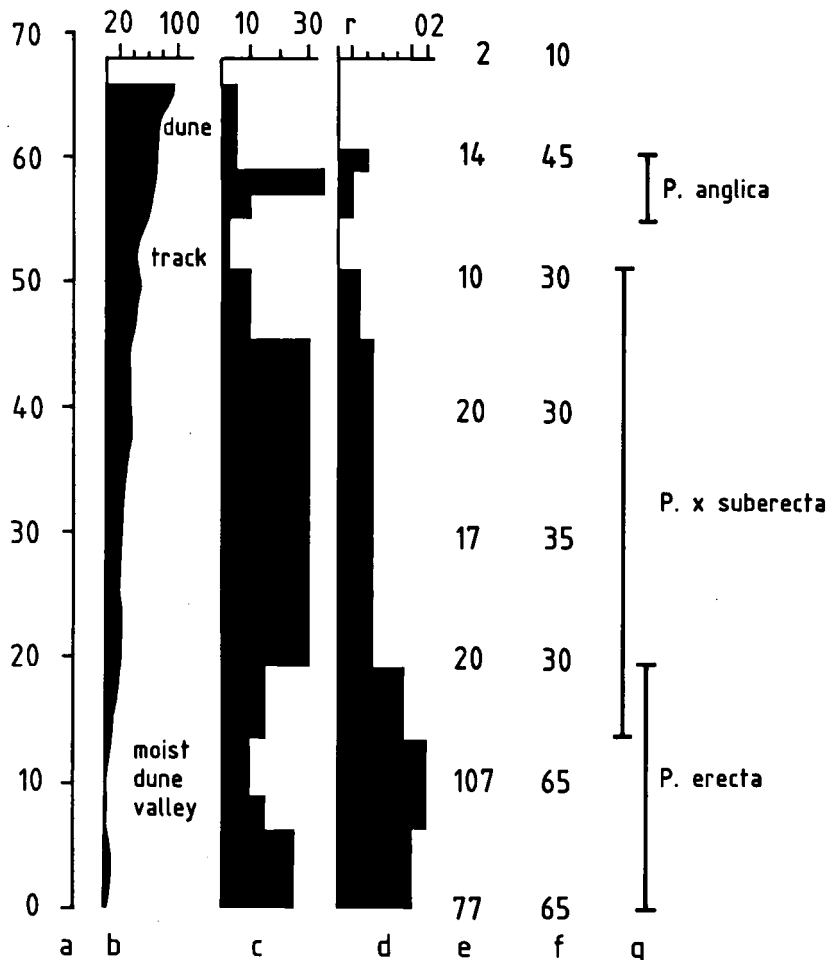


Fig. 3. Example of ecological differentiation between *P. erecta*, *P. anglica* and *P. × suberecta*: a distance scale (m), b relative height of ground level (cm), c height of vegetation (cm), d coverage of *Potentilla* taxa (r, p, a, m, 01, 02), e soil water (dry weight %), f organic matter (volume %), g range of the 3 *Potentilla* taxa. The situation relates to the Schiermonnikoog populations.

investigated only *P. reptans* was found.

P. reptans occurred frequently in large numbers on clay and humic sand on moderate moist to dry places in open habitats. The vegetation in which it occurs was relatively low and usually strongly influenced by human agency. As accompanying species were found: *Rumex crispus*, *Cirsium arvense*, *Plantago major*, *Leontodon autumnalis*, *Taraxacum* spec. (sect. *Taraxacum*), *Trifolium repens*, *Potentilla anserina*, *Ranunculus repens*, *Arrhenatherum elatius*, *Dactylis glomerata*, *Festuca arundinacea*, *Poa trivialis* and *Lolium perenne*.

P. erecta grew on peat or humic sand, often in large quantities, frequently

in swamps and moist dune valleys. Usually it occurred in relatively high vegetation which was relatively undisturbed. As accompanying species could be recorded: *Betula pubescens*, *Salix repens*, *Erica tetralix*, *Phragmites australis*, *Calamagrostis epigejos*, *Juncus effusus*, *Agrostis canina*, *Rumex acetosa*, *Lychnis flos-cuculi*, *Mentha aquatica*, *Lotus uliginosus*, *Drosera rotundifolia*, *Hydrocotyle vulgaris*, several *Sphagnum* spec. and *Polytrichum commune*.

P. anglica was often found in fairly small quantities on humous sand, peat or (peaty) clay, usually in moderate moist situations, rather frequent on slopes of dunes and dikes. The vegetation concerned was comparatively low, more or less influenced by man, and composed of: *Rubus* spec., *Chamaenerion angustifolium*, *Plantago lanceolata*, *Galium album*, *Rumex acetosella*, *Luzula campestris*, *Holcus lanatus*, *Agrostis stolonifera*, *Poa pratensis*, *Festuca rubra*, *Corynephorus canescens* and *Carex arenaria*.

In populations, *P. × suberecta* occupied often about 30–50% of the total of *Potentilla* plants. Its ecological preference is about the same as that found in *P. erecta*, but it showed a wider amplitude, which is illustrated in fig. 3. Particularly *P. × suberecta* occurred in drier places and higher vegetation (e.g. *Salix* scrub).

P. × mixta was found twice in small numbers. Near Bilthoven the plants were growing along an oligotrophic ditch, in a fairly moist situation. In the Lage Vuursche population *P. × mixta* occurred along a wood track, in a moderate moist soil.

3.3. Morphology of the hybrids *P. × suberecta* and *P. × mixta*

The morphology of the species *P. anglica*, *P. erecta* and *P. reptans* is adequately described in the literature (see also table 1). Therefore, in this paper attention is paid only to the morphology of the two hybrids.

P. × SUBERECTA

The description is based on 20 living specimens out of the populations Streefkerk, Reeuwijk, Nieuwkoop and Ilperveld.

Stems: procumbent, strongly dichotomously branched, 5 (1–38) per plant and 25 (10–60) cm in length.

Radical leaves: 11 (6–40) per plant, 40% three-merous, 30% four-merous and 30% five-merous; middle leaflet 15 (8–29) × 12 (6–20) cm.

Cauline leaves: 7 (3–13) per stem, 80% three-merous, 15% four-merous and 5% five-merous; middle leaflet 17 (8–31) × 8 (4–15) mm.

Stipulae: 7 (3–16) × 5 (2–14) mm, with 3 (1–7) lobes, incised for 3/5 (0–4/5).

Petioles: 6 (2–16) mm in length.

Penduncles: 40 (16–50) mm in length.

Flowers: 3 (0–8) per stem, four-merous and 12 (9–14) mm in diameter.

Calyx leaves: 4 (3–5) mm in length.

Corolla leaves: 5.5 (3.5–7.5) mm in length.

Carpels: 13 (6–28) per flower.

Pollen fertility: 47 (0–80)% of the pollen well developed.

Table 2. Pollen fertility, number of carpels and percentage of these developing into fruits, based on 20 specimens of each *P. erecta*, *P. anglica* and *P. × suberecta*, all from the Schiermonnikoog populations. A standard deviation is given with each value.

| | pollen fertility (%) | number of carpels | carpels developing into fruits (%) |
|-----------------------|----------------------|-------------------|------------------------------------|
| <i>P. erecta</i> | 94 ± 3 | 8 ± 2 | 76 ± 22 |
| <i>P. anglica</i> | 91 ± 4 | 25 ± 6 | 77 ± 16 |
| <i>P. × suberecta</i> | 34 ± 14 | 15 ± 5 | 45 ± 23 |

Fruit setting: 5 (1–10) carpels per flower developing into fruits, with a mean of 38%.

Roots at the nodes: in less than 3% of the nodes.

In table 2 the numbers of well developed pollen and fruits of *P. × suberecta* are compared to those of the parental species *P. anglica* and *P. erecta*. In most of the morphological characters *P. × suberecta* ranges from *P. anglica* to *P. erecta*, which is illustrated in fig. 4.

P. × MIXTA

Of *P. × mixta* a concise description is given, because only 9 voucher specimens were available, all from the population at Bilthoven.

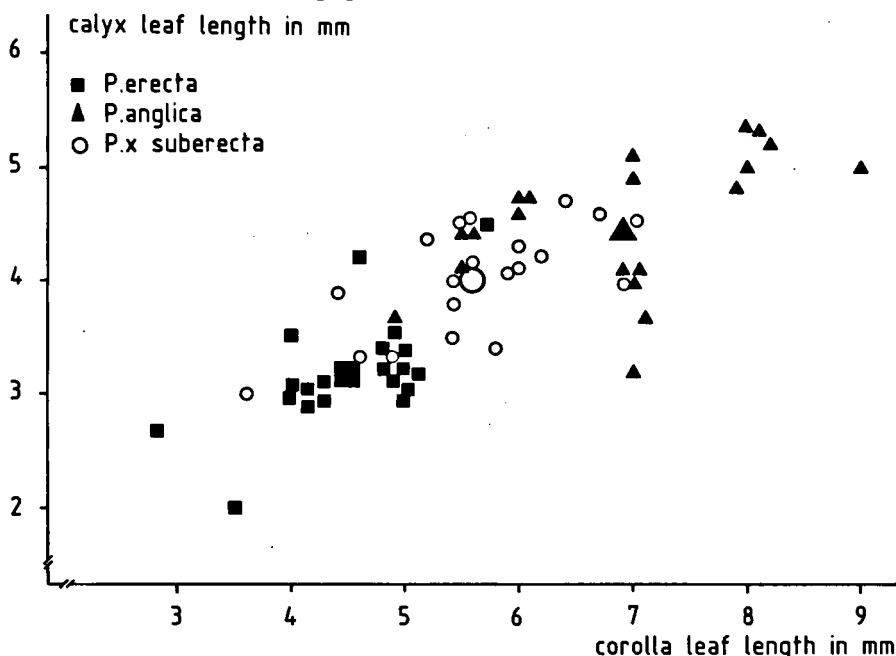


Fig. 4. Scatter diagram of the corolla/calyx ratio for 20 specimens of each *P. erecta*, *P. anglica*, and *P. × suberecta*, all from the Schiermonnikoog populations. Larger symbols give the mean value for each.

Table 3. Number of air borne pollen of *P. erecta*, compared with the pollen from some other groups, for five populations. Numbers between brackets are percentages.

| | number of <i>P. erecta</i> pollen | number of Gramineae pollen | number of pollen from other groups | total number of pollen |
|-----------|---|----------------------------------|--|---------------------------|
| Voorne 1 | 1 (1) | 112 (90) | 12 (10) | 125 (100) |
| Voorne 2 | 0 (0) | 72 (90) | 8 (10) | 80 (100) |
| Voorne 3 | 22 (71) | 9 (19) | 0 (0) | 31 (100) |
| Hilversum | 11 (24) | 34 (72) | 2 (4) | 47 (100) |
| Egmond | 27 (26) | 14 (13) | 64 (61) | 105 (100) |
| total | 61 (16) | 241 (62) | 86 (22) | 388 (100) |

Stems: more or less creeping, sparsely branched, 3 (1–6) per plant, 40 (15–70) cm in length.

Radical leaves: c. 3 per plant, five-merous; middle leaflet 20 (15–25) × 11 (10–15) mm.

Cauline leaves: 7 (3–11) per stem, 15% three-merous, 15% four-merous and 70% five-merous; middle leaflet: 16 (7–30) × 7 (4–13) mm.

Stipules: 8 (4–13) × 2 (1–14) mm, usually entire, seldom incised for 1/5–4/5 and with 2 or 3 lobes.

Petioles: 40 (10–145) mm in length.

Peduncles: 60 (25–120) mm in length.

Flowers: 6 (0–9) per stem, 30% four-merous and 70% five-merous and 18 (12–23) mm in diameter.

Calyx leaves: 6 (4–8) mm in length.

Corolla leaves: 8 (5–10) mm in length.

Carpels: 70 (50–95) per flower.

Pollen fertility: for a few living plants c. 100% ill-developed pollen was found.

Roots at the nodes: in c. 25% of the nodes.

3.4. Functioning of the pollen

In order to get insight in the functioning of the pollen in relation to species maintenance and hybridization, experiments and observations were carried out in five *P. erecta* populations (Voorne 3 ×, Hilversum and Egmond).

3.4.1. Functioning of the pollen in relation to fertilization

In each of the five populations mentioned 15 microscopic slides were placed during a bright, slightly blowy day from 10 h a.m. to 8 h p.m.. The pollen obtained in this way was analysed along three stretches over each slide. Therefore, table 3 in which the results are summarized gives relative numbers of pollen. From this table it can be concluded that the proportion of *P. erecta* pollen is on an average of 16% and this means that wind pollination may take place.

Pollination by insects was also investigated. Insect behaviour during pollina-

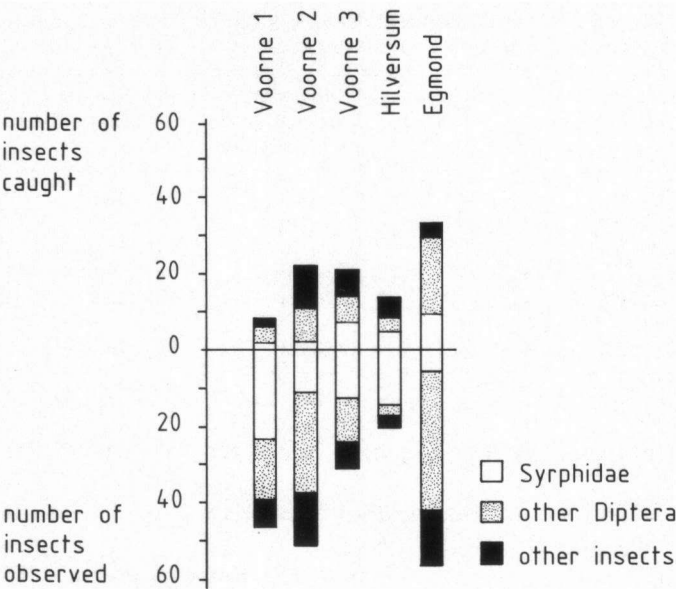


Fig. 5. Number of insects caught, respectively observed only, in five *P. erecta* populations.

Table 4. Number of insects from different families, with and without *P. erecta* pollen, caught during one day of observation in 5 *P. erecta* populations. Also is given the share of the *P. erecta* pollen in the total pollen found on the insects. The first six insect families are the most important ones.

| | Number of caught insects with <i>P. erecta</i> pollen | Number of caught insects without <i>P. erecta</i> pollen | Share of <i>P. erecta</i> pollen in the total pollen on the insects (%) |
|----------------------|--|---|--|
| Syrphidae | 21 | 4 | 78 |
| Muscidae | 9 | 2 | 95 |
| Tachnidae | 8 | — | 93 |
| Chloropidae | 8 | 4 | 91 |
| Thripidae | 7 | 12 | 100 |
| Ephydriidae | 3 | 2 | 50 |
| Diptera unidentified | 3 | — | 83 |
| Apidae | 2 | — | 28 |
| Formicidae | 1 | 1 | 92 |
| Trichogrammatidae | 1 | 1 | 100 |
| Cantharidae | 1 | — | 100 |
| Salticidae | 1 | — | 100 |
| Stratiomyiidae | 1 | — | 50 |
| Delphacidae | — | 2 | 0 |
| Agromyzidae | — | 1 | 0 |
| Calliphoridae | — | 1 | 0 |
| Cecidomyiidae | — | 1 | 0 |
| Nabidae | — | 1 | 0 |

Table 5. Development of mature fruits, in percentages of the total number of carpels, for 30 flowers in each group, for five populations of *P. erecta*.

| | fruits in emasculated, not pollina- ted, envelop- ed flowers (group 1) | fruits in emasculated, self polli- nated, envel- oped flowers (group 2) | fruits in emasculated, cross polli- nated, envel- oped flowers (group 3) | fruits in open pollinated, just finished, enveloped flowers (group 4) | fruits in open pollinated, normal developed flowers (group 5) |
|-----------|---|--|---|--|--|
| Voorne 1 | 0 | 9 | 47 | 83 | 89 |
| Voorne 2 | 0 | 7 | 25 | 80 | 89 |
| Voorne 3 | 0 | 4 | 16 | 72 | 80 |
| Hilversum | 0 | 4 | 28 | 79 | 79 |
| Egmond | 0 | 2 | 56 | 61 | 75 |

tion was observed, and as far as possible the pollinating insects were caught. Per population in principle one plant was observed during a sunny day between 10 h. a.m. and 6 h. p.m.. The numbers of both observed and caught insects are given in *fig. 5*. The pollen on the insects caught was analysed by means of a light as well as a scanning microscope. It proved that quite a number of insects carried high percentages of *P. erecta* pollen (see *table 4*). The following active pollinators were identified: *Syrphus vitripennis*, *Metasyrphus corollae*, *Sphaerophoria scripta*, *Melanostoma scalare*, *Platycheirus albimanus*, *Pyrophæna granditarse* and *Chrysogaster hirtella* (Syrphidae); *Orthellia cearion* (Muscidae); *Siphonia spec.* (Tachinidae); *Rhagomycha fulva* (Cantharidae); *Myrmica sabuletti* (Formicidae); *Bombus terrestris*, *Bombus pascuorum* (Apidae); *Bianor canescens* (Salticidae). Some of these pollinating insects were also reported by HEGI (1922) for central Europe, while WIKLUND (1977) observed the butterfly *Aricia nicias* in central Sweden.

3.4.2. Functioning of the pollen in relation to fructification.

Flowers were emasculated and bagged-in. The seed set was studied after pollination with pollen of another flower of the same plant, after cross pollination, or pollination was left undone. Pollination was carried out twice on two consecutive days. Moreover, some flowers were bagged-in just before anthesis started. The results of these experiments are summarized in *table 5*. After comparison of the results in group 3 and 4 it appeared that the seed-set was not negatively influenced by the surrounding bags. Emasculation without cross-pollination did not result in the formation of ripe achenes (cf. group 3 and 4; and field observations). From these results it can be concluded that *P. erecta* does not reproduce agamosperously (group 1) and that either self-fertilization or pseudogamous reproduction results in the formation of mature and viable fruits (group 2). Seed formation in *P. erecta* is largely the result of cross-pollination and fertilization (group 3). The same holds true for other taxa of the Tormentillae.

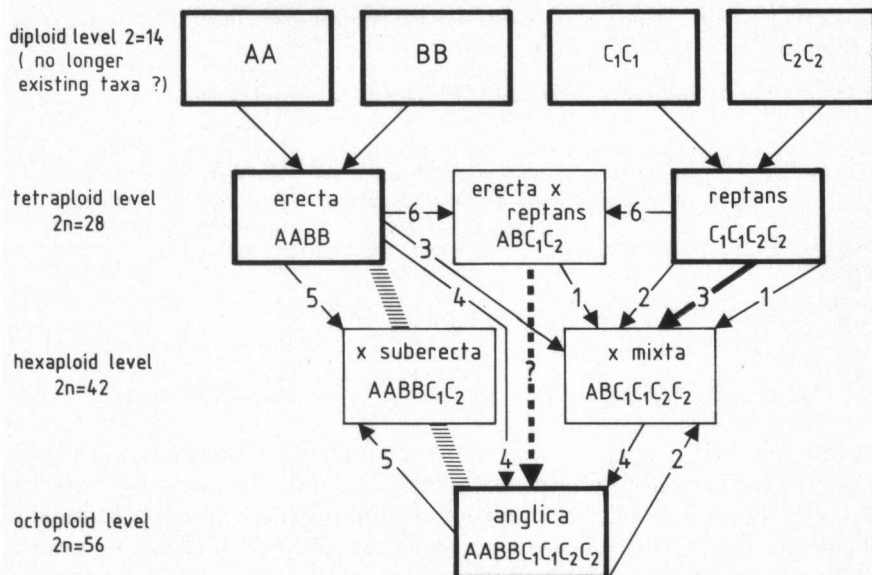


Fig. 6. Relationship and hybridization pathways in *Tormentillae*. A, B, C₁, and C₂ are symbols for the genomes of four related taxa, and C₁ and C₂ for two closely related ones. Bold lined rectangles represent species, thin lined ones hybrids. Thin arrows mean contribution of a reduced chromosome set via pollen or egg cell, heavy arrows contribution of an unreduced egg cell. Same numbers refer to corresponding contributions of pollen grain or egg cell and conversely. Query in combination with interrupted line means that this way may be possible, but is not proved. Shaded band, finally, stands for specimens with intermediate chromosome numbers, connecting taxa of different ploidy level.

4. DISCUSSION AND CONCLUSIONS

Potentilla reptans (2n=28), *P. erecta* (2n=28) and *P. anglica* (2n=56) are of common occurrence in The Netherlands (pers. comm. E. J. Weeda, Rijksherbarium, Leiden). Our study revealed that also *P. × suberecta* (2n=42) is fairly common. It is usually found in habitats where both parents occur or where at least one of the parents is present. In contradiction with MATFIELD's (1972) findings for England *P. × mixta* (2n=42) appears a very rare plant in The Netherlands. *P. erecta × reptans* was not found and obviously this hybrid does not occur.

We prefer to apply the biological species concept for the *Tormentillae*: all specimens with 2n=42 and a low pollen and fruit fertility are assigned to *P. × mixta* or *P. × suberecta*, although some of these plants are morphologically nearly identical with *P. anglica* or *P. erecta*, respectively. Others (e.g. SCHWENDENER 1970; SKALIŃSKA & CZAPIK 1958) do not agree with such a delimitation which is primarily based on fertility and instead use morphological character combinations for the delimitation of these taxa. In our opinion this approach precludes an exact establishment of the degree of hybridization in mixed popula-

tions. Moreover, exact identification of Tormentillae specimens sometimes is only possible with the aid of data on chromosome number and fertility degree.

Backcrossing of *P. × suberecta* with the parental species was found in 15 specimens, which is c. 25% of all *P. × suberecta* – like plants. So, to a certain extent introgression and hybrid-swarms are present, mainly towards *P. anglica*. In mixed populations *P. × suberecta* often has an important part probably because it produces a fairly large number of fertile pollen and fruits. In addition, it is more robust, and it shows a wider ecological amplitude.

Based on literature data, as given the introduction, mainly MATFIELD & ELLIS (1972) and SCHWENDENER (1970), and on our own observations we constructed the following scheme with regard to hybridization in the Tormentillae (fig. 6).

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