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FLOWERING AND SEX EXPRESSION IN *ACER* L.

A BIOSYSTEMATIC STUDY

(with a summary in Dutch)

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ABSTRACT

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A review and an analysis is given of flowering and sex expression in *Acer*. The process of sex differentiation was studied in physiological experiments and could be influenced by accelerated flowering and by removal of ♀ flower buds just after bud break. The paper further includes notes on the morphology, mainly of the reproductive organs, and a study of floral morphogenesis. A taxonomic study led to the division of *Acer* into 15 sections, partly subdivided into 2–3 series. Of these series, two, *Ukurunduensia* and *Wardiana*, are described for the first time. A key to the sections and series is added. The evolution of *Acer*, especially of its flowering and sex expression, and of its morphological characters, is discussed. Notes on sex expression in related genera are included.

Descriptors: morphology, floral morphogenesis, sex differentiation, taxonomy, evolution, *Dipteronia*, *Aesculus*, *Koelreuteria*.

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CONTENTS

1. GENERAL INTRODUCTION

1.1. THE GENUS ACER

The *Aceraceae* contain two genera: *Acer* and the small genus *Dipteronia*. The family belongs in the *Sapindales*, and is rather closely related to the *Sapindaceae* and *Hippocastanaceae*.

The maples are trees and shrubs characterized by opposite leaves and a winged schizocarpic fruit, the samara. The leaves show a large variability within the genus. Most common are 3- or 5-lobed leaves, while also unlobed, 7-13-lobed, trifoliolate, palmatifoliolate or pinnate leaves occur (see fig. 4).

Several taxa are heterophyllous, i.e., they produce more than one leaf type. Most maples are deciduous; (partly) evergreen taxa occur in the southern areas of the genus in Asia and Europe. The number of bud scales varies from 2 to 9–13 pairs.

The rather small flowers are produced on various types of inflorescences (see fig. 1), arising from mixed both terminal and lateral buds and sometimes exclusively from leafless lateral buds. They mostly have a 5-merous perianth, 8 stamens and a bicarpellate pistil, variations in these numbers occur (see 2.3). The flowers are functionally unisexual caused by abortion of the pistil or incapacity of the anthers to shed pollen.

Both types of unisexual flowers are found on the same tree (monoecy) or on different trees (dioecy). Flowering usually takes place simultaneously with, or shortly after, bursting of the mixed buds. Most maples are entomophilous, a few taxa are anemophilous.

The samaras often develop parthenocarpically; in dioecious taxa this is always the case. The seeds lack endosperm and the embryos have green cotyledons.

The genus contains 111 (-ca. 150) species arranged by the present author in 14 sections (see 6.4 and table 1). To establish the exact number of species further revisional work is needed. Several taxa, particularly from China, Indochina and the Mediterranean region are as yet insufficiently known.

Acer occurs in the major part of the temperate regions of the northern hemisphere. Most southward maples occur in the southern Himalayas and in the mountains of Malaya, Indonesia, (e.g. Java, Borneo, Celebes, Timor) and the Philippines (Luzon). This means that only in Indonesia does the genus cross the equator to about S.L. 10°.

In America maples may be found as far south as Guatemala; in N. Africa one or two species grow in the Atlas, while in W. Asia N. Israel is the most southern area. The northern boundary lies between N. Lat. 45°C. in Asia and about N. Lat. 65° in western N. America and N.W. Europe. The distribution of the taxa is summarized in table 1. The present major centre is China where 12 of the 14 sections and half the number of the species occur. Japan with 20 species in 10 sections is also a very important centre. Asia has representatives of all sections, altogether about 90% of the species. N. America houses 9 sections including 10 species. In Europe only 3 sections comprising 12 species are represented.

Maples are generally found in mountainous regions. In the S.E. Himalyas they may occur up to an altitude of 3300 m. With the exception of the evergreen taxa of the Mediterranean Region they mainly prefer rather humid habitats in mixed forests and thickets, along streams and on slopes. Several taxa like some shade and have trees of second size. Only a few species dominate in the top layer of the forests in the natural stands (e.g. *A macrophyllum* and *A. saccharum*). Although maples are trees of medium size, they can reach heights of above 40 m.

Maples have already been cultivated for over thousands of years. Several species are valued for their timber. The sap of a number of species, particularly *A. saccharum*, is tapped during early spring for the production of the famous maple syrup. Even more important is their application as ornamental trees and shrubs, and in road plantings. The large variability of the leaves in shape and colour, the coloured branches, the beautiful yellow, bronze and red autumn colours make the maples much appreciated trees. The species, which are most common in cultivation and of which many cultivars were selected mainly originate from Japan, Europe and N. America. Although the Chinese species form half the genus and include some with very attractive trees, they have been of secondary importance for cultivation until now.

TABLE 1. Geographic distribution of *Acer* species per section

Section	Europe W. Asia	C. and E. Asia	China	Japan	Western N. America	Eastern N. America	total area
I *Acer*	8	1	1			1(+1)	10(+1)
II *Platanoidea*	4	13(+6)	9(+5)	2			15(+6)
III *Palmata*		29(+11)	20(+9)	5	1		30(+11)
IV *Macrantha*		15(+4)	7(+2)	4(+1)		1	16(+4)
V *Parviflora*		3	1	3		1	4
VI *Trifoliata*		5(+4)	5(+4)				5(+4)
VII *Rubra*		1		1		2	3
VIII *Ginnala*	1	2(+2)	1(+1)	1(+1)			3(+2)
IX *Lithocarpa*		4(+6)	3(+4)	1	1		5(+ 6)
X *Negundo*		2	1	1	1	1	3
XI *Glabra*		4(+1)	1(+1)	1	1		5(+1)
XII *Integrifolia*		8(+6)	8(+6)				8(+6)
XIII *Indivisa*		1		1			1
XIV *Hyptiocarpa*		3(+4)	2(+3)				3(+4)
Genus ACER	13	90(+44)	59(+34)	20(+2)	4	6(+1)	111(+45)

( ) insufficiently known taxa: (sub) species or synonyms

1.2. FLOWERING AND SEX EXPRESSION

Numerous studies of the flowering process in higher plants have already been made, but the enormous diversity of specialisation is responsible for the fact that the knowledge of flowering in many taxa is still very incomplete. This also applies to the processes, which have led to the development of unisexual flowers and finally of male and female plants.

Complete dioecy occurs in less than 5 per cent of the higher plants (YAMPOLSKI and YAMPOLSKI, 1922). This strongly contrasts with large animal groups (vertebrates, arthropads), which are strictly unisexual. Possibly limiting factors have suppressed the evolution to unisexuality in the *Angiospermae*.

In the case of monoecy unisexuality of the flowers is only conducive to cross-pollination if self-pollination is prevented or reduced by spatial segregation (herkogamy) or by asynchronous anthesis of the male and female flowers (dichogamy) (FAEGRI and VAN DER PIJL, 1966). While the sexuality of the flowers may vary, pollination itself must remain ensured, for instance pollinators may not show preference to flowers of one sex only (e.g. pollen collectors).

Both complete dichogamy, which may be regarded as a functional dioecious system, and dioecy demand synchronisation of anthesis of the male and female flowers and a certain density of the populations.

In many taxa of higher plants entomophily is partly or completely replaced by anemophily. The latter development required a large number of specialisations of the flowers: high pollen/ovula ratio; small, smooth and dry pollen grains, which do not adhere to each other; exposed anthers and stigmas, resulting from a reduction of the perianth or elongation of the filaments; drooping flowers with thin pedicels; enlarged stigmatic surfaces. The transport of pollen needs adaptations for air circulation around the inflorescences, which may be realized by a flowering period before leaf development or an arrangement of the inflorescences on the periphery of the plants. Wind pollination further needs the presence of wind, a low air humidity and an open, sparse vegetation. Consequently anemophily, particularly with trees, mainly occurs in certain habitats (WHITEHEAD, 1969). Anemophily is often found in monoecious and dioecious taxa, and is sometimes regarded as a starting point towards an evolution to full dioecy (STEBBINS, 1951).

In *Acer*, of which the present species are said to date from the Pliocene (POJARKOVA, 1933), about 15 per cent of the species are completely dioecious. Only one fully dioecious species is completely anemophilous. The remaining taxa all have unisexual flowers and the populations consist of monoecious and dioecious flowering individuals in various quantities. They are supposed to show phases in the evolution of the now dioecious taxa. An analysis of flowering and sex expression in these taxa may supply useful data towards a better insight into the evolutional trends of the maples.

1.3. SCOPE OF INVESTIGATIONS

This study was initially taken up to make an analysis of flowering and sex expression in *Acer* and carried out by observations on living specimens in botanic gardens and elsewhere. To complete the observational data for the whole genus the uncultivated taxa were studied from herbarium specimens in some of the largest herbaria (Chapter 3).

Several interesting observations and insufficient descriptions of morphological characters in the literature led to a detailed study of the morphology, especially of the reproductive organs (Chapter 2).

To study the mechanism of the variable sex expression some physiological experiments were made to obtain information about the sex differentiation (Chapter 5). The latter study required a knowledge about the whole period of flower morphogenesis (Chapter 4).

During his study the writer gradually became more and more interested in the taxonomy and the phylogenetic trends of the genus. The results of the study of flowering and sex expression and the morphology were useful aids for a revision of the intrageneric classification (Chapter 6) and a discussion of the evolution within the genus (Chapter 7).

2. MORPHOLOGY

2.1. INTRODUCTION

A study of the taxonomy and phylogeny of *Acer* requires a knowledge of many morphological characters. Some of these, mainly of the flowers and inflorescences, were found to be insufficiently described for a number of taxa.

The wide variability of the morphology of flowers and inflorescences was studied and tabulated to facilitate an approach to their possible evolution. The evolutionary trends are discussed in chapter 7.

A separate section is devoted to the terminology of the sex expression (2.4). Some confusion in literature about the terminology used is caused by a varying morphological and physiological (functional) approach.

Some attention is given in the present chapter to the parthenocarpic fruit, (2.5.2).

2.2. THE FLOWER

2.2.1. *The number of floral parts*

Usually *Acer* flowers have 5 sepals, 5 petals, 8 stamens and a bicarpellate ovary. Sometimes 4-merous flowers with 4 stamens occur. Small deviations from these basic numbers of floral parts frequently occur, especially as regards the stamens. Average numbers of 5, 10 or 12 stamens are also found. In an inflorescence there is often a tendency to a reduction in the number of stamens in the last flowers to open, and 4-merous flowers may be found instead of 5-merous ones. The range of these variations within the genus is shown in table 2.

In dioecious taxa female flowers may lack stamens. However, male flowers mostly have at least traces of an ovary, but only BUCHENAU (1861) reported the presence of abortive ovaries in male flowers of *A. negundo*. Other authors, e.g. WRIGHT (1953), HALL (1954) MOMOTANI (1961) and OGATA (1967), did not observe them.

Male specimens of three dioecious species were studied at the Wageningen Botanic Gardens (Wag. B.G.). The male flowers of *A. cissifolium* (no. 1763) and *A. negundo* (no. 8310, no. 13166) nearly always had two unconnated carpels (see fig. 32). Sometimes the abortive ovary consisted of one carpel, which might appear as a scrufulous hair in the centre of the disc (*A. cissifolium* no. 1763, *A. carpinifolium* no. 1773).

The flowers of *A. carpinifolium* (no. 1773) usually had no visible rudimentary ovaries when flowering. Yet in young flower buds undifferentiated primordia were often visible (see also 4.2)

Tricarpellate ovaries were frequently found. They were also reported by several authors, among them BUCHENAU (1861), PAX (1885), DAYTON (1945),

Table 2. Variation of certain morphologic characters in *Acer*.

Section	Series	number of floral parts			position of the disc[1]	inflorescences		nutlet[4]	parthenocarpic tendency[5]	folding manner of the cotyledones [6]	leaf type[7]	pairs of bud scales
		sepals	petals	stamens		type [2]	arrangement[3]					
I *Acer*	*Acer*	5	5	8	E	II	I	C	m	i	6	5–10
	Monspessulana	5	5	8	E	II	I	C	s	i	5,6,(9)	8–12
	Saccharodendron	5	0(–2)	8	E	II	II	C	s	i	5,6	6–9
II *Platanoidea*	*Platanoidea*	5	5	8	A	II	I	F	m	a	5,6,9	5–8
	Pubescentia	5	5	5	A	II	II	F	m	a	5,6	6–10
III *Palmata*	*Palmata*	5	5	8	E	I	I	C	m	i	6,7	4
	Sinensia	5	5	8	E	I	I	C	w–m	i	5,6,7	4
	Penninervia	5	5	8	E	I	I	C	w–m	i	10	4
IV *Macrantha*	*Tegmentosa*	5	5	8	I	III	II	F,(C)	m	a	5,6,9	2
	Wardiana	5	5	8	A	I	I	F	m?	?	5	2
V *Parviflora*	*Parviflora*	5	5	8	I	I	I	C	w	i	5–6	2
	Ukurunduensia	5	5	8	A–I	I	I	FV	w	a	5–6	2–3
	Distyla	5	5	8	A	I	I	C	m	i	10	2
VI *Trifoliata*		5–6	5–6	10–13	E–A	II–III	II	C	s	i	3	11–15
VII *Rubra*		5	0(–3),5	4–6	–,I	IV	IV	C	w	a	5–6	4–7
VIII *Ginnala*		5	5	8	E	II	II	FV	m	a	4,5,9	5–10
IX *Lithocarpa*	*Lithocarpa*	5	5	8	A	III	IV	CV	s	i	5,6	8–12
	Macrophylla	5–6	5–6	9–12	A	II	I	C	s	a	6	5–8
X *Negundo*	*Negundo*	4–5	–	4–5	–	III–V	III	FV	s	a	2	2–3
	Cissifolia	4	4	4	A	III	III	FV	s	a	3	2
XI *Glabra*	*Glabra*	5	5	8	A	II–III	II	FV	s	a	3–5	2–4
	Arguta	4	4	4–6	A	III	II,IV	FV	s	a	5,9	2–3
XII *Integrifolia*	*Trifida*	5	5	8	E	II	I	C	s	i	5,9	4–8
	Pentaphylla	5	5	8	E	II	I	C	?	?	8	4–8
XIII *Indivisa*		4–5	4–5	4–6	A	III	I	F	s	a	10	9–13
XIV *Hyptiocarpa*		5	5	5–12	A	II–III	IV	C	w	?	10	7–11

[1] E = extra-staminal, A = amphi-staminal, I = intra-staminal; [2] see fig. 1; [3] I = terminal, II = term. + lateral, III = lateral, partly mixed buds, IV = lateral; [4] C = convex, F = flat, V = veined: [5] w = weak, m = moderate, s = strong: [6] i = incumbent; a = accumbent; [7] see fig. 3.

HALL (1951), RATIV (1960), HAASIS (1963) and KABULOV (1966). ULBRICH (1928) suggested that the present bicarpellate condition was derived from a tricarpellate (found in the related *Hippocastanaceae* and *Sapindaceae*). Occasionally a further increase in the number of carpels was found. BUCHENAU (1861) observed a 4-carpellate fruit of *A. saccharinum*. WYDLER (1857) found fruits of *A. platanoides* with 4 and 5 carpels. LANGNER (in PAX; 1885) observed 4-carpellate and BOUCHÉ (1879) 4-, 5- and 8-carpellate fruits of *A pseudoplatanus*. HAASIS (1963) observed 4-, 5,- 6-, and 10-carpellate fruits of *A. macrophyllum*.

The present author observed 4- to 11-carpellate fruits on cultivars of *A. pseudoplatanus* ('Costorphinense' no. 8382, 'Leopoldii' no. 11460, 'Purpureum' no. 11476).

PAX (1885), KOIDZUMI (1911) and HALL (1951) supposed that the 5-merous flowers originally had 5-carpellate ovaries. However PAX reported about asymmetric and irregular arrangement of ovaries with three or more carpels.

The present author also found that when ovaries consisted of four or more carpels, such ovaries always showed fasciation and had 2–3 connate styles (separate canals). Even fasciated flowers with a still higher number of carpels were observed (*A. henryi*, Gimborn Arb., 13 carpels; *A. ginnala*, Wag. B.G. no. 12481, 17 carpels), but these flowers had several free styles. Such polycarpellate flowers showed an increase in other floral parts too. In flowers of *A. pseudoplatanus* 'Purpureum' no. 11476 up to 8 sepals and petals and 21 stamens were found.

The irregular arrangement and the fasciations of ovaries with 4 or more carpels may indicate that a tricarpellate ovary is more original than a 5-carpellate.

2.2.2. *The occurrence of a connate perianth*

Comments in literature on a connate perianth, as found in some species, are often contradictory. The corolla in particular was not always closely examined.

In the case of *A. diabolicum*, a dioecious species, the male flowers have a connate perianth (KOIDZUMI, 1911; MOMOTANI, 1962; OGATA, 1967). REHDER (1927, 1960), however, supposed that the petals were wanting.

Several authors reported that in flowers of *A. saccharum* the corolla is wanting (SARGENT, 1892; REHDER, 1927, 1960; HALL, 1951; WRIGHT, 1953; GABRIEL, 1968; MURRAY, 1970). HALL remarked: 'there are no petals or vestiges of petal traces'.

OGATA (1967) supposed that the petals were united with the sepals. His supposition was partly based on observations of more than 5-lobed perianths, partly on the monoecious condition since he found that all other species with a reduced corella were dioecious.

From studies of herbarium specimens it may be concluded that the perianth is mostly 5-lobed, but several specimens had flowers with a 6- to 8-lobed perianth. One specimen was found which had some flowers with free of partly free petals (Orishamy, Vasey s.n. (K)). The perianth was split opposite the free petal. The petals, unlike the remaining part of the perianth, were not hairy. It appeared that the corolla may be completely reduced in some local subspecies and varieties of *A. saccharum*, but that nevertheless in a few specimens one or more free petals may still be present in the otherwise connate perianth.

The flowers of *A. saccharinum* too are mostly considered as apetalous (HEIN, 1907; HAAS, 1933; REHDER, 1927, 1960; MURRAY, 1970), but BUCHENAU (1961) sometimes found flowers with one or more petals. PAX (1902) reported the presence of 1–3 petals. According to OGATA (1967) the corolla was 'usually' wanting. On several of the specimens studied at the Wag. B.G. a varying number of flowers with 1–3 free petals were found. The length of these petals rather differed. In female flowers these petals enlarged until after the receptive period (see fig. 27,2). The perianth was always split opposite the free petal. These splits could also be observed in the absence of free petals (see fig. 27,3). Such flowers also occurred in some other clonal varieties in the Wag. B.G.: 'Elegant' no. 7810, 'Lutescens' no. 13167, and no. 12288 (named *A. rubrum* var. *pallidiflorum*). In other morphological characters these trees also are very similar. Very probably they are all synonymous with *A. saccharinum* 'Schwerinii'.

It may be possible that a connate perianth was the result of a further compression of the floral axis. This compression brought the sepals and petals together into one whorl in the same way as observed for the two stamen whorls (see 2.2.4).

2.2.3. *Distinction of calyx and corolla*

Within the genus the corolla shows, besides reduction and fusion with the calyx, distinct variations in shape and colour. A number of taxa have flowers with white or whitish petals, highly contrasting with the green or reddish sepals (sections *Palmata* and *Parviflora* and series *Cissifolia*). The most striking contrasts are present in species of the southern range of section *Palmata:* e.g. *A. campbellii*, *A. erianthum*, *A. laevigatum*, *A. sinense* and *A. tonkinense* (see fig. 16). Their flowers have recurved red or reddish sepals and 3- 5-lobed, white petals, which are rolled inwards. The long smooth petals in series *Ukurunduensia* and *Cissifolia* contrast markedly with the small inrolled, hairy sepals.

In most of the remaining taxa the petals have about the same yellowish, greenish or, occasionally, reddish colour as the sepals. Usually there are only small variations in size, hairiness and curvature between them.

As in several species the petals of male flowers elongate during anthesis, male flowers grow larger in diameter than female flowers (see fig. 17, 18 and 21).

2.2.4. *The arrangement of the stamens*

Literature dealing with the arrangement of the stamens is rather contradictory. The rather irregular whorl of 8 stamens was thought to have developed from two whorls of 5 stamens (EICHLER, 1878; PAX, 1885; KOIDZUMI, 1911; HALL, 1951). Either a diplostemonous or an obdiplostemonous arrangement can be supposed and the position of the reduced stamens wants an explanation.

PAYER (1857) provided pictures of the development of the stamens on flower buds of *A. tataricum*. In the first of the corresponding figures 5 stamen primordia are visible. They are situated nearly opposite the sepals, and the spaces between them already indicate the place of three remaining stamens. The second figure shows their primordia in the open places of the first whorl.

BUCHENAU (1861) observed the simultaneous development of one whorl with 8 stamens in *A. pseudoplatanus*.

According to CHATIN (1874) 5 stamens appear simultaneously in the *Aceraceae*. Their position was in some cases described as exactly episepalous. From the remaining stamens two were developed roughly opposite the lateral petals and the third opposite one of the hindmost petals. They were arranged outside the first whorl, so he found an obdiplostemonous arrangement and a reduction of two epipetalous stamens. He also observed obdiplostemony in the related genera *Aesculus* and *Koelreuteria* and in the *Malpighiaceae*.

His observation on the related *Sapindaceae* and the *Malpighiaceae* led EICHLER (1878) to accept obdiplostemony also for the *Aceraceae*. In his diagram of *A. pensylvanicum* the 8 stamens are arranged in one whorl and the places of the two reduced stamens are in alignment with the two carpels. This 'Abortlinie' is said to run always through sepal 2 suggesting that in each whorl one stamen is reduced.

PAX (1885) suggested that the original diplostemonous arrangement was changed into an apparent obdiplostemonous one by the development of the disc.

HAAS (1933) studied the development of the androecium in three species: *A. pensylvanicum*, *A. pseudoplatanus* and *A. tataricum*. An obdiplostemonous arrangement and a reduction of two not adjacent epipetalous stamens was observed. He made a diagram of *A. pensylvanicum*. The stamens always appeared simultaneously, but their arrangement in one whorl followed at an early (*A. pseudoplatanus*) or late phase of development. The epipetalous stamens of *A. tataricum* developed slower than the episepalous. HAAS also observed a retarded elongation and dehiscence of the three epipetalous stamens of male *A. circinatum* flowers. The last mentioned observation was previously made by PAX (1885) for *A. japonicum* and *A. hookeri*.

HALL (1951) studied the floral anatomy of 9 species of *Acer*. With one exception he observed that the stamen traces all arose from the stele at the same level and in what appeared to be a single whorl. In the case of *A. pensylvanicum* he once found the traces of the 3 epipetalous stamens at a lower level than the others. He suggested that any difference in level of the two whorls that might have existed in ancestral forms had been lost by compression of the floral axis. He never observed traces of reduced stamens.

The observation made by the present author on young flower buds of *A. campestre*, *A. platanoides*, *A. pseudoplatanus* and *A. tataricum* supported an obdiplostemonous arrangement and a reduction of 2 epipetalous stamens as reported by CHATIN and HAAS. Occasionally 5 epipetalous stamens were found. It was, however, not possible to confirm PAYER's observations of reserved locations for the three epipetalous stamens. During the further development of the androecium and the formation of the disc, the stamen arrangement became indistinct. The development of the disc may have a strong influence on the ultimate arrangement as was observed in *A. spicatum* flowers. If these flowers have 8 stamens, 3 episepalous stamens are completely enclosed at their base by a large discus lobe. The other two episepalous discus lobes, which are never adjacent, are rather small. The remaining 5 stamens are all apparently epipetalous and inserted between the 5 discus lobes. Flowers with 10 stamens have 5 episepalous stamens, each enclosed by a discus lobe at their base. These observations seem to give an indication of a reduction of episepalous stamens. However, the staminal arrangement in this case seems to have been changed by the development of these episepalous discus lobes through which 2 episepalous stamens were shifted to the position of the reduced epipetalous stamens.

2.2.5. *The honey disc*

Depending on the insertion of the stamens, the location of the disc may be extrastaminal, intrastaminal or, sometimes rather indistinctly, amphistaminal. This variation was pointed out by several taxonomists as an important distinguishing mark for classification. PAX (1885) introduced the terms *Extrastaminalia* and *Intrastaminalia*. However they were only used for half the genus and not maintained in his monograph of 1902. KOIDZUMI (1911) classed all PAX's sections under the *Extra-* and *Intrastaminalia*. This general division was also adopted by REHDER (1927) and MOMOTANI (1962) in their keys for the genus. NAKAI (1915) followed KOIDZUMI, but placed the section *Platanoidea* in a separate group: the *Circumstaminalia*.

In table 2 the mode of staminal insertion is indicated for each taxon, except series *Negundo* and *A. saccharinum*, of which the flowers lack a disc.

The amphistaminal disc shows a wide morphological variation and the taxa having this disc are often not closely related. The disc margin may be entire (the stamens inserted in its centre, e.g. section *Platanoidea*), but may also be lobed (the stamens in the centre of the lobes: series *Ukurunduensia*), or more or less enclosed between the lobes; series *Distyla* and *Pubescentia*; (see fig. 23.10). The disc is usually glabrous but in some species it is more or less pubescent. Pubescent discs were reported for *A. campbellii*, *A. erianthum*, *A. garrettii*, *A. reticulatum*, *A. sinense* and *A. tutcheri* (SCHWERIN, 1901; MERRILL, 1932 and FANG, 1939). The present author observed densely pubescent discs in the flowers of *A. tonkinense* (see fig. 16). The pubescence remained after flowering. Slightly hairy discs were observed on *A. fabri*, *A. laurinum*, *A. nipponicum* and *A. wardii*.

For remarks on the evolution of the disc see (7.3.2.4)

2.2.6. *The style and stigmas*

The size of the stigmas on flowers of some taxa seems clearly related with the anemophilous condition of these maples, e.g. *A. negundo*, *A. rubrum* and

A. saccharinum. These stigmas are lengthened by a full split in the style enlarging the pollen-receptive surface.

The flowers of several other taxa may also have a rather short style and rather long stigmas. Especially if such taxa flower before or during the unfolding of the leaves the proportion of wind pollination may be rather important, e.g. sections *Macrantha, Trifoliata, Lithocarpa* and *Acer (A. monspessulanum, A. opalus* and *A. saccharum)*.

Within a species wide variations in style and stigma length occur. Flowers of *A. macrophyllum* for example usually have a short style and long stigmas, but on some herbarium specimens flowers with long styles and short stigmas were found (Columbia River, Surksdorf s.n. (P, BM) Victoria, Fletcher 146 (BM). Similar variations were observed in the sections *Acer, Ginnala* and *Platanoidea.*

2.2.7. *The pollen*

Studies of morphological characters of pollen of about 30 species were made by HELMICH (1963). She distinguished colpate and colporate pollen grains. The latter occurred less frequently (series *Palmata* (4 species studied), *Parviflora* and *Ukurunduensia*; *A. glabrum* subsp. *douglasii* and *A. tataricum*). The studied material was not further identified. It is very likely that the specimen labelled *Acer douglasii* (Oregon, Anonymus 941607 (MO)) is *A. circinatum*. The pollen of this specimen resembled that of *A. circinatum*, a species from the same area, and differed widely from pollen of *A. glabrum*, of which *A. douglasii* is considered to be a subspecies. She noticed a rather wide intraspecific variation of the pollen grains. The pollen grain diameters of anemophilous species were not smaller than those of the mainly entomophilous species from North America: *A. negundo* (22–35μ), *A. rubrum* (26–30μ), *A. saccharinum* (28–34μ) against *A. circinatum* (22–35μ), *A. glabrum* (25–31μ), *A. macrophyllum* (36–44μ), *A. pensylvanicum* (22–25μ), *A. saccharum* (25–37μ) and *A. spicatum* (18–24μ).

The present author studied pollen of ♂ and ♀ flowers of some species. It was observed that the anthers of ♀ flowers of monoecious species always contained pollen. Slides with fresh pollen in water were studied with a microscope and pollen diameters were measured. The mean diameter of pollen grains of ♂ flowers was larger than that of ♀ flowers of the same specimen. Pollen of ♀ flowers was mostly rather heterogeneous, had varying diameters and was more or less transparent: *A. campestre* 'Elsrijk' (no. 17863) ♂ flowers, dia. 43–50μ; mean dia. 46μ; ♀ flowers 33–47μ; mean dia. of single ♀ flowers varied between 38–41μ; *A. platanoides* (no. 18077) ♂ flowers 1–2 days before anther dehiscence: dia. 33–43μ, mean dia. of single flowers 40–42μ; ♀ flowers 23–43μ and 33–40μ respectively; no further variations; *A. maximowiczianum* (no. 794): ♂ flowers dia. 33–50μ, average of single flowers 40–46μ; ♀ flowers dia. 20–40μ and 27–30μ respectively.

Specimens of the same species may show large variations: *A. campestre* 'Nanum' (no. 1766), ♂$_{\mathrm{I}}$, dia. 23–40μ, mean dia. 30μ; 'Elsrijk', ♂$_{\mathrm{II}}$, dia 43–50μ, mean dia. 46μ.

The pollen of ☿ flowers of *A. rubrum* (no. 1757) was relatively more heterogeneous and transparent than that of ♂$_{II}$ flowers: mean dia. 33 and 35μ respectively.

See also the results of germination studies in 5.6.

2.3. THE INFLORESCENCE

2.3.1. *Classification*

The compound inflorescences are widely variable in their structures, but have hardly been studied in detail. In literature the inflorescences are described as corymbose, paniculate, racemose, umbellate, paniculate-racemose, paniculate-corymbose, etc.. Yet ALMSTEDT (1933; quotation HALL, 1951) proposed a phylogenetic scheme for the American species, which was mainly based on the external appearance of the inflorescences (see 7.3.1). The inflorescences of ♂ *A. negundo* were mostly described as fasciculate (PAX, 1902; OGATA, 1967; MURRAY, 1970). BUCHENAU (1861) considered them as simple racemes. BELOSTOKOV (1961) studied the generative shoot development of *A. negundo* and made detailed schemes of the compound inflorescences (see 2.3.2.). HAAS (1933) described the inflorescences of *A. circinatum* as bifalcate. TROLL (1957), however, proved the cymous inflorescences of *A. circinatum* and *A. palmatum* to be scorpioid.

The present author found in *Acer* 5 basic types of inflorescences, which are shown in figure 1. The arrangement in this figure as a phylogenetic scheme will be discussed later (see 7.3.1). The distribution of these types in the genus is shown in table 2. The most difficult part of the inflorescence to describe is the ramification of the rachis. The lowest secondary axes are opposite, in accordance with the opposite leaf position of the vegetative shoot. This secondary branching passes into scattered branching, sometimes with a transitional zone with one or two whorls with 3–8 secondary axes. If the lowest secondary axes are rather long, their tertiary branching can correspond to that of the secondary of the rachis. The continued branching of the secondary axes can result in monochasia consisting of cincinni: type I (see fig. 1). These cincinni are generated by branching on the node of the lowest bracteole (α-prophyl) of the secondary, tertiary and following axes. The number of flowers of these cincinni varies from 2 to 14 (*A. tonkinense*; Kwangsi, Steward & Cheo 152 (BM), *A. nipponicum*; Hondo, Wilson 7201 (K); Yaska-bushi, Watanable s.n. (K)). In the case of small cincinni (2–4 flowers) the criterion for classification in this type is the absence of any other mode of tertiary branching of the inflorescences. According to the length of the rachis two extremes can be distinguished: type Ia with a very short rachis (*A. circinatum*) and type Ib with a very long rachis (see fig. 1).

Type II represents the most common inflorescence found in *Acer*. Most secondary axes carry two or more tertiary axes (see fig. 1). These tertiary axes can only occasionally develop into small cincinni with 3–4 flowers. As in type I extremes with a very short and elongated rachis can be distinguished (see fig.

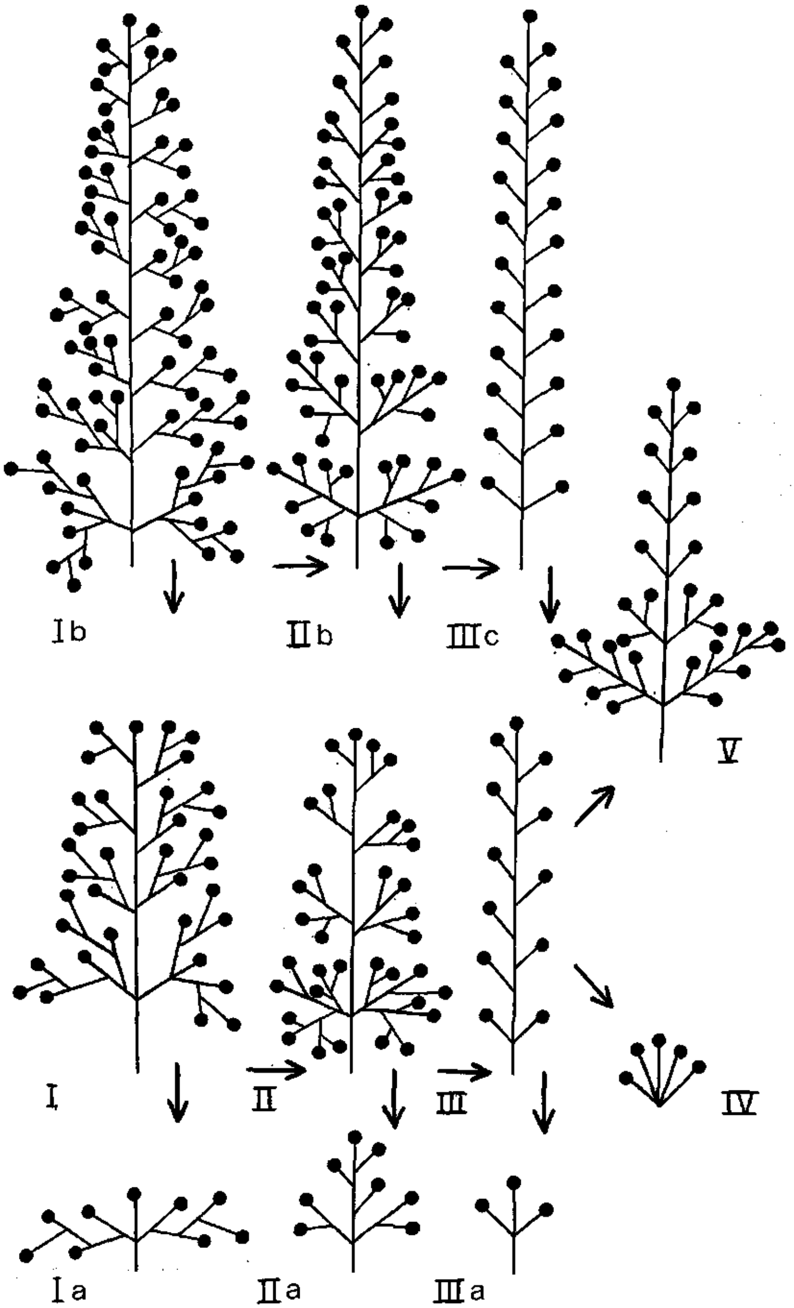

FIG. 1. Basic types of inflorescences in *Acer*: I. compound infl. with cincinni; II. ibid.: cincinni reduced; III. racemes; IV. umbel; V. compound raceme; (a = reduced rachis, b = elongated rachis). The arrows indicate possible evolutional trends.

1). The inflorescences of *A. pseudoplatanus* arranged under type IIb have tertiary axes, which are partly inserted on the rachis by shortening of the secondary axes (see fig. 6 and 8).

The inflorescences of type III are racemes with a terminal flower. Extremely short and long racemes are classed as types IIIa and IIIb. Type IV is a sessile umbel, which is only found in the section *Rubra* (see fig. 1 and 25–27 and table 2).

Type V represents a compound raceme, which can be found in ♂ specimens of *A. negundo*. The puzzling classification of the inflorescences of *A. negundo* is closely connected with the development of the generative shoot (see the next paragraph).

2.3.2. *Terminal and lateral inflorescences*

The position of the inflorescence on the generative shoots and the number of companion leaves should also be considered. These characteristics were used for classification, e.g. by REHDER (1905), OGATA (1967) and MURRAY (1970). OGATA summarized in a table 4 groups according to the position of the inflorescence on the shoots. With some modifications this division is given in table 2.

In most taxa inflorescences from mixed buds of the previous year predominate. Depending on the pairs of companion leaves OGATA divided these taxa into two groups. In the present study the occurrence of lateral inflorescences was also considered. In group I lateral inflorescences are carried almost exclusively on vigorous long shoots of the previous year, those of group II not. As a consequence section *Trifoliata* could be placed in group II, while OGATA gave this section an intermediate position.

The female specimens of series *Arguta* have given rise to much confusion. According to REHDER (1905) the inflorescences of those specimens are terminal on short lateral two-leaved branches. OGATA (1967) spoke of mixed lateral buds and MURRAY (1970) of mixed terminal buds.

The present study revealed that the inflorescences mainly developed from terminal buds on short shoots but also from lateral buds on mostly long shoots (group II).

Groups III and IV exclusively develop inflorescences from lateral buds. The distinction between these groups lies in the possible occurrence of more or less mixed buds in group III. These mixed buds have leaflets, which mostly drop prematurely. In section *Negundo* they predominantly occur on female specimens.

The development of inflorescences on one-year-old long shoots of *A. negundo* was closely studied by BUCHENAU (1861) and BELOSTOKOV (1961). The latter made very detailed schematic drawings of the variations. Female specimens had one, and in the middle of robust generative shoots sometimes 2–3 racemes from one lateral bud. In the latter case the complementary inflorescences were formed in the axils of the outermost pair of bud scales. Each single inflorescence was subtended by 2–3 pairs of bud scales and usually had one pair of leaflets. The male specimens of *A. negundo* mostly had lateral buds with two pairs of bud scales. Lateral buds in the middle of robust generative shoots could have complementary inflorescences in the axils of both pairs of bud scales. Each single inflorescence was subtended by only one pair of bud scales, which again could have an axillary ramification.

According to BUCHENAU all these ramifications within the lateral buds of male specimens led to a number of single inflorescences. BELOSTOKOV considered the bud scales as bracts of a compound inflorescence, that is a compound receme, delimited in the present study as type V (see 2.3.1). Instead of an inflorescence the bud scales of lateral buds sometimes had axillary leaf buds. The reverse development, axillary inflorescences and a terminal leaf bud was also found. It was observed on male specimens of *A. cissifolium*. On these specimens the single racemes were subtended by one pair of bud scales.

This continued branching within the lateral buds of generative long shoots is very pronounced in the section *Rubra*. BUCHENAU (1861) and HAAS (1933) described these developments. In 1–3 pairs of the outermost bud scales of a lateral bud axillary inflorescences could be formed. Each single inflorescence became finally subtended by about 5 pairs of bud scales. Through the pressure of the developing axillary inflorescences the outermost bud scales of the original lateral bud were pushed away and dropped before the winter.

2.3.3. *The abcsission of blown (male) flowers*

After flowering all male flowers fall off immediately. The female flowers of all taxa show at least initially parthenocarpic development of the ovary (see 2.4). In most monoecious taxa the ♂ flowers drop with their pedicels. In the case of a terminal flower on a further branched axis an abcsission layer is formed just above the uppermost lateral axis. Above the mark of the fallen pedicels some taxa show a small ring. This ring represents a scar of a bract. The rings are rather clearly visible on fruiting inflorescences in the series *Platanoidea* (see fig. 13).

In series *Penninervia*, *Sinensia* and *Ukurunduensia* and in the genus *Dipteronia* only part of the pedicels of the ♂ flowers drop (see fig. 23 and 33). The abcission layer is probably formed in the node of the uppermost bractlet (β-prophyl). The place of the abcission is indicated by a small articulation of the pedicel. Hairy pedicels have differently arranged hairs on this node (*A. spicatum*). Above the fertile lowest bractlet (the α-prophyl), which is also the bract of the side axis, both axes partly fused.

The abscission of the ♂ flower in series *Palmata* and *Wardiana* is preceded by a shedding of anthers or stamens, while in series *Ukurunduensia* the petals and stamens drop first (see fig. 23). The inflorescences from ♂ representatives of dioecious taxa drop off whole. There is no abscission of single flowers. In the same way rather small, completely ♂ inflorescences of monoecious species will be shed, e.g. section *Trifoliata* and series *Tegmentosa*. Large ♂ inflorescences shed the withered flowers first, while the entire inflorescence together with the remaining flowers is shed at the end of the flowering time.

In section *Rubra* a cluster of ♂ inflorescences, developed from one lateral bud, falls off whole.

In the case of ♂ inflorescences from mixed lateral buds, as occasionaly found in section *Negundo* and series *Arguta*, the whole lateral axis including a pair of small leaves also drops.

2.4. SEXUALITY IN ACER

2.4.1. *The sexuality of the flowers*

Morphological and functional variations in the sexuality of *Acer* flowers were first mentioned by LINNÉ. In his Genera Plantarum, ed. 2 (1742) he described in detail the occurrence of two types of bisexual flowers on the same inflorescence. In the first the anthers were indehiscent. In the second the pistil was abortive[1]. In ed. 5 (1754) he added a third type, namely male flowers. These flowers had pistils with a split stigma but without a germ and style.

JUSSIEU (1789) also distinguished three types of flowers, viz. bisexual flowers, and male and female flowers as a result of abortion. However, to segregate these types proves to be rather difficult because this needs the distinction between bisexual and female flowers.[2]

Several authors described the functional ♀ flowers as bisexual (= hermaphrodite or perfect) and used, often in the same context, the term female for these flowers (e.g. PAX, 1902; MOMOTANI, 1961, OGATA; 1967).

SCHNEIDER (1907) distinguished, probably on account of the length of the filaments, species with ☿ and ♀ flowers. Examples of the first were *A. ginnala*, *A. monspessulanum*, *A. platanoides* and *A. pseudoplatanus* and examples of the second *A. palmatum*, *A. rubrum*, *A. saccharum* and *A. sikkimense*.

KOIDZUMI (1911) indicated all functional ♀ flowers as ☿, even those of *A. carpinifolium*, which have rudimentary stamens. However for *A. maximowiczianum* he described ♀ flowers despite the clearly visible stamens of the flower pictured.

One and a half centuries after LINNÉ's remark the two types of (functional) ♂ flowers were also described by MAC LEOD (1894). The ♂ flowers had 'in the centre an imperfect pistil, which appeared as a little brush of white hairs (first stage?) or as a white hairy little bump (ovary), bearing two or more or less abortive styles on its top (second stage?)', (see also 3.3. series *Acer* 1). HAAS (1933) made the same observations on *A. platanoides*. He described very clearly the occurrence of these two types during flowering. In the consecutive

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[1] 'Flores, in eadum umbella Hermaphroditi, saepe duplicis generis: inferiores Hermaphroditi feminei, quorum antherae non dehiscunt, sed pistillum mox in fructum excrescit; superiores Hermaphroditi masculi, quorum antherae pollen pluunt, pistilla vero non accrescunt, sed decidunt.'

[2] 'Flores... flexubus infoecundis aut abortivis masculi aut feminei hermaphroditis mixti aut distincti.'

phases of ♂ and ♀ flowers, the first type (♂$_{I}$) was always found before a phase of ♀ flowers and the second type (♂$_{II}$) after a ♀ phase.

However some authors described the ♂$_{II}$ flowers as ☿ (Jussieu?, 1789; Scholz, 1960), most authors distinguished only one morphological type of ♂ flowers. Klaehn (1959) remarked in this connection: 'If we wish to split hairs we might call the male flower perfect because a rudimentary pistil is present in the bottom of the corolla. This would indicate that at one time this flower was also perfect'. In spite of the small dimensions of these abortive pistils the present author will show in following chapters that in the case of monoecious specimens the differentiation of ☿ flower buds, both to ♀ and ♂, can still take place a few days before flowering. In this paper the sexuality of the flowers will be indicated by their function, where needed detailed morphological descriptions are added. Additionally the distinction of the two morphological types of ♂ flowers (♂$_{I}$ and ♂$_{II}$) will be used.

The criterium for a ♀ flower will be the inability to release pollen. In case of pollen release, fertile or not, the flowers will be considered as ☿. This kind of bisexuality was described by Haas (1933) for *A. rubrum* (see 3.3 VII 4) and by Gabriel (1962) for *A. saccharum* (one flower!).

A fourth possibility are flowers without functional sexual organs. Such flowers are defined as asexual flowers. They were first described by Wahlenberg (1820) for *A. platanoides.*[3] Weiser (1973) noticed them on *A. pseudoplatanus* specimens.

2.4.2. *The sex expression of inflorescences*

As pointed out in the preceding paragraph the sexuality of flowers will be based on the functional sexual organs. If all flowers of an inflorescence are ♂, ♀ or ☿ such inflorescences are accordingly indicated by ♂, ♀ or ☿. Androgynous inflorescences mostly show (second order) dichogamy, either by protandry, protogyny or duodichogamy (Stout, 1928). The latter condition is shown in figure 2. For describing the sex expression, however, a rather simple notation will be used, following Wittrock (1886) (See 3.2). The occasional polygamous inflorescences had not yet been indicated by a special code.

2.4.3. *The sex expression of plants*

Plants with exclusively ♂ and ♀ flowers as a consequence of their genetic constitution will be indicated as ♂ and ♀ individuals. Otherwise such individuals will be described as ♂ or ♀ flowering specimens, the addition 'flowering' indicating that the genetic constitution is neither male nor female. Plants showing both sexes will be called monoecious. Occasionally plants were polygamous, because some flowers functioned as ☿.

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[3] 'Flores triplicis generis... 2) *Hermaphroditorum* (potius Neutrorum) stamina petalis triplo breviora anthesis vix dehiscentibus, stylus longitudine staminum, stigma viridia, germen e nectario emersum sed plerumque abortiens'.

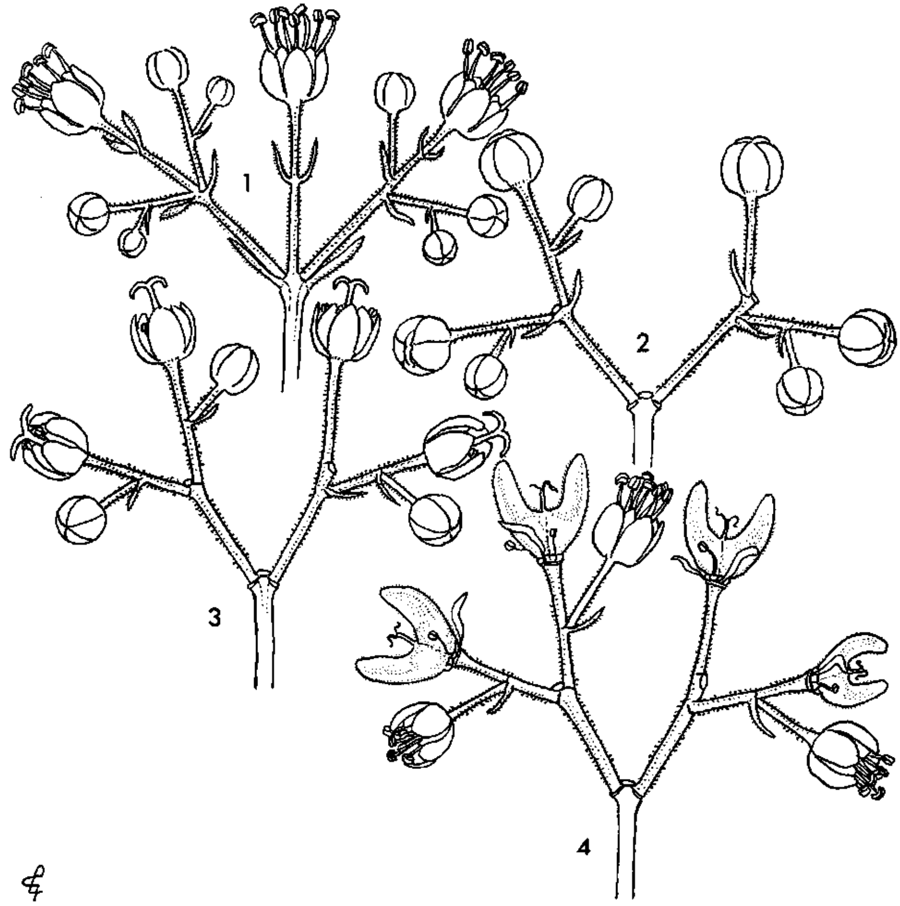


FIG. 2. *Acer ginnala* Maxim.: Duodichogamy: 1–4. part of infl. (standardized), complete segregation of ♂ and ♀ phases (2×): 1. ♂$_{I}$ phase, 2. start of ♀ phase: stigmas of ♀ fl. become visible, ♂$_{I}$ fl. dropped, 3. ♀ phase, 4. ♂$_{II}$ phase: withered stigmas of ♀ fl. (Wag. B.G. no. 8330).

2.4.4. *The sex expression of species*

Species with ♂ and ♀ individuals are defined as dioecious. Because of the morphological ☿ appearance of the functional ♀ flowers of some dioecious species, various authors used the term androdioecious (e.g. PAX, 1886; KOIDZUMI, 1911; FANG, 1939; REHDER, 1927; MOMOTANI, 1962; OGATA, 1967; MURRAY, 1970).

Most species of the genus have mainly monoecious individuals with a variable number of ♂-flowering specimens, while occasionally ♂ individuals may be found. In literature these species are mostly described as andromonoecious (e.g. PAX, 1886, 1902; OGATA, 1967; MURRAY, 1970) or andropolygamous (e.g. MAXIMOWICZ, 1880; KOIDZUMI, 1911; FANG, 1939; REHDER, 1927; MOMOTANI, 1961).

According to DARWIN (1877) andromonoecy concerns individuals with ♂ and ☿ flowers, while andropolygamy represents a condition with ♂ and andromonoecious individuals. From a morphological point of view andropolygamy is the correct term, but for a functional approach no term was found in literature.

The stages between complete monoecy and dioecy may be indicated as *imperfect monoecy*. This imperfectness may be caused genetically or environmentally. Some levels of imperfect monoecy will be distinguished below (see 3.5).

2.5. THE FRUIT

2.5.1. *The shape of the fruit*

The indehiscent, winged fruits are composed of two one-seeded mericarps (samara dicarpellata).

In addition to the number of bud scales OGATA (1967) considered the shape of the locules of the fruits as the most important distinguishing character for the delimitation of the 26 sections he adopted. Main characters of the locules are their being convex or flat and their smooth or veined surface (see table 2).

MOMOTANI (1961) remarked that the shape of the locules is closely connected with the shape of the seeds. It shoud be noted that the fruit is often parthenocarpic, and then remains hollow. In case of a normal development, the embryo fills up the cavity in the fully grown fruit. With or without a low parthenocarpic tendency there may be a reciprocal influence of fruit and embryo on their ultimate shape.

MOMOTANI (1961) especially studied the anatomy of the pericarp. The kinds of cell layers varied from 3 to 5. Structures sometimes changed during the development of the pericarp, e.g. *A. negundo* showed an increase from 3 to 5 cell layers.

2.5.2. *The parthenocarpic fruit*

The ♀ flowers of all species have a tendency to develop into parthenocarpic fruits. This tendency is very evident in dioecious species. Their seedless fruits are practically indistinguishable from seed bearing fruits. Special observations were made on fruits with one seedless and one seedy mericarp. It appeared that parthenocarpy exist in varying degrees.

1. **weak**: the seedless mericarp of a fully grown fruit is small and sometimes also sheds earlier. Such fruits are found in case of a very rapid development of one embryo after flowering. This embryo always fills the cavity of the nutlet entirely. Unfertilized flowers usually drop after flowering. Plants without fertilized flowers can show a light parthenocarpic development of the fruits till about one month after flowering. Species with such a low parthenocarpic tendency belong for example to section *Rubra* (fig. 3.3 and 3.4), *Hyptiocarpa* (fig. 3.5) or *Palmata* (e.g. *A. tonkinense*, fig. 3.2.) The same condition was observed in *Dipteronia* (fig. 3.1). See further table 2. Occasional observations

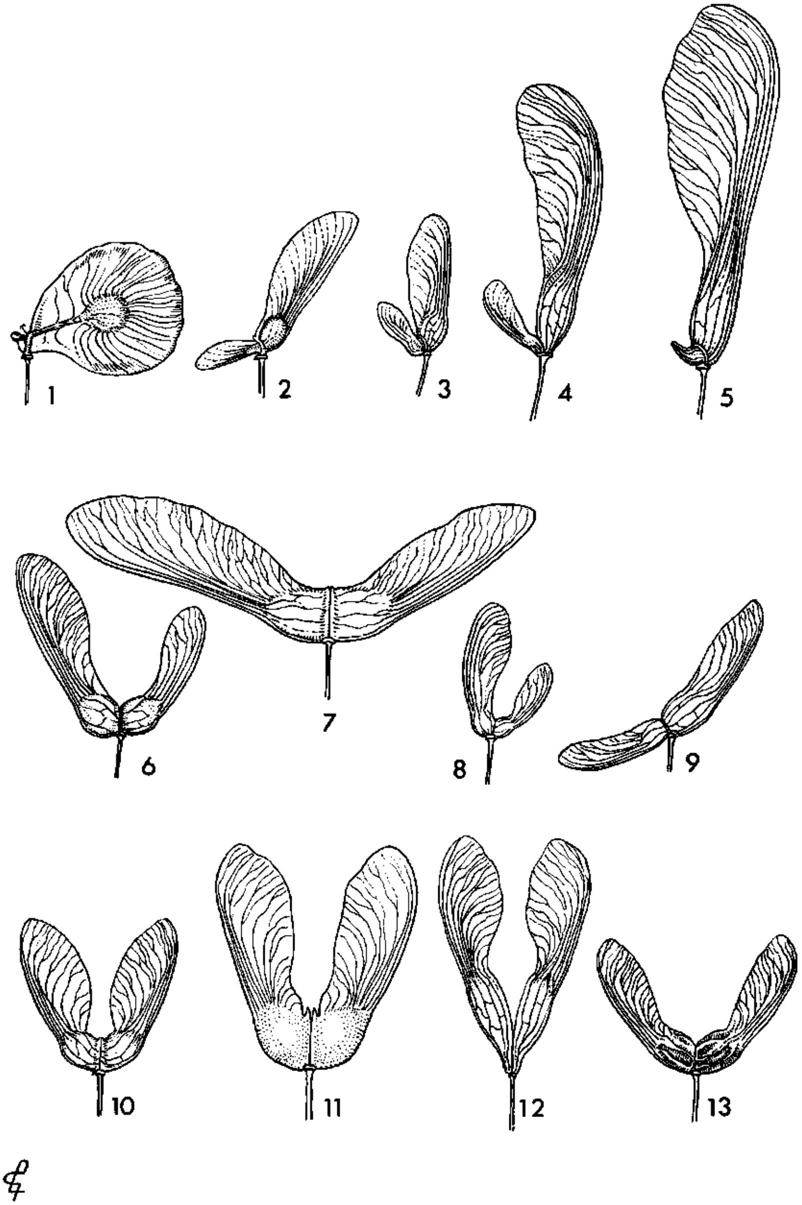


FIG. 3. One-seeded samaras with various degrees of parthenocarpic development of the seedless mericarp (${}^{5}/_{6}$ ×): 1–5. parthenocarpic tendency weak; 6–9. ibid. moderate; 10–13. ibid. strong. 1. *Dipteronia sinensis* Oliv. (De Jong 266); 2. *Acer tonkinense* Lecomte (Stewart & Cheo 613); 3. *A. rubrum* L. (de Jong 405); 4. *A. saccharinum* L. (Mazzeo 995); 5. *A. laurinum* Haskarl (Chun & Tso 43433); 6. *A. pseudoplatanus* L. (De Jong 330); 7. *A. platanoides* L. (De Jong 634); 8. *A. rufinerve* S. & Z. (De Jong 503); 9. *A. circinatum* Pursh. (De Jong 211); 10. *A. opalus* Mill. (De Jong 83); 11. *A. griseum* (Fr.) Pax (De Jong 260); 12. *A. negundo* L. (Vrugtman 1067); 13. *A. stachyophyllum* Hiern. (De Jong 350).

indicated that the low parthenocarpic tendency is caused by a strong competition of the vegetative shoots. Removal of the leafy buds from some branches of *A. rubrum* 'Tilford' no. 15922 before flowering led to the development of a number of empty parthenocarpic fruits of normal size on these branches.

2. **medium**: The seedless mericarp of fully grown fruits has a relatively smaller wing and nutlet than the seed bearing carpel. Unfertilized flowers have a parthenocarpic development for variable periods of time. A small part are shed within some weeks of flowering, while the majority drop in June.

In case of few or no fertilized flowers, part of the parthenocarpic fruits can stay on the tree till the autumn, but they are always smaller than seed bearing fruits.

A moderate tendency for parthenocarpy is the most common condition in the genus *Acer*. It is for example present in series *Acer* (fig. 3.6.), *Platanoidea* (fig. 3,7) and *Tegmentosa* (fig. 3.8). See table 2.

3. **strong**: The empty mericarp is indistinguishable from the seed bearing one of the same fruit.

If there is no pollination 50–100 per cent of all the ♀ flowers develop into parthenocarpic fruits of the same size as normal seed containing fruits.

Occasional observations on a partly hand-pollinated specimen of *A. henryi* at the Zuiderpark in 1971 revealed a competition between the various fruits. Premature drop of parthenocarpic fruits predominantly occurred on the hand pollination inflorescences. Unpollinated inflorescences had numerous parthenocarpic fruits of normal size, while the few parthenocarpic fruits of the pollinated inflorescences were a little smaller than the seedy fruits.

This strong parthenocarpic tendency is especially common in dioecious taxa and also rather frequently occurs in taxa with many paired bud scales. See table 2 and fig. 3, 10–13.

2.6. THE SEED

2.6.1. *The embryo*

The manner of folding of the cotyledons in the endospermless seed has been regarded as an important taxonomical character (PAX, 1885; REHDER, 1905; SCHNEIDER, 1907; MOMOTANI, 1961.) REHDER distinguished incumbent and accumbent cotyledons. Incumbent cotyledons will mostly be found in convex locules, while accumbent cotyledons will mostly be found in concave locules. See table 2.

Some species having accumbent cotyledons and convex locules, (e.g. *A. macrophyllum* and *A. rufinerve*, lack this correlation but their fruits contain some brown material partly filling the cavity within the locules (OGATA, 1967)). The embryos have green cotyledons, except those of species with very thick-walled fruits, e.g. section *Trifoliata*.

2.6.2. *Two-seeded mericarps*

In each locule two ovules are found, but only one develops after fertilization. Occasionally mericarps with two seeds were observed: *A. griseum* (Zuiderpark) *A. heldreichii* (Kew Bot. Gardens, Belmonte no. 14324) *A. maximowiczianum* (Gimborn Arb.), *A. pensylvanicum* (Wageningen).

CARLE and YAWNEY (1972) reported on twin seedlings of *A. saccharum* caused by polyembryony. Both seeds were enclosed by one single testa. The frequency found was very low, CARLE and YAWNEY report 0.0015%. From a single tree 24 mericarps had two seeds, each seed enveloped by a testa, out of 30.000 seed bearing samaras (frequency 0.08%).

2.6.3. *Seed germination*

Nearly all species show epigeal germination. *A. saccharinum* is commonly known as an exception because of hypogeal germination.

The present author also observed hypogeal germination of *A. truncatum* seeds. The cotyledons of the latter remained underground or emerged partly. Sometimes they emerged entirely, but in all cases they remained enveloped by the pericarp. Seeds of various origins were tested: Kew Gardens no. 275, H.B. Taschkent and Zuiderpark.

Seeds of *A. rubrum* and *A. saccharinum* germinate immediately at maturity in early summer. Very often they will germinate while laying on the soil. In the case of *A. saccharinum* there is hardly any development of the hypocotyl. It was observed that some days after germination the thick green cotyledons became visible, while the cotyledons of seeds germinating on the soil surface shed the pericarp and spread as in epigeal germination.

The seeds of most species will germinate in the next spring. An exception are the seeds enveloped by thick ligneous pericarps, which take another year to germinate, but a sowing of the green fruits in early autumn sometimes led to germination in the following spring (e.g. *A. maximowiczianum*).

2.7. THE BUD SCALES

OGATA (1967) considered the number of bud scales as very important to the systematics of the genus. In 1961 MOMOTANI made a rough division into three categories. OGATA refined this scheme distinguishing, somewhat arbitrarily, 5 categories. It appears that only some limiting numbers can be indicated, e.g. up to 4 pairs of bud scales, and 5 or more pairs. Some sections have a fixed number of 2, 3, or 4 pairs of bud scales, but with increasing numbers the variations become wider and more frequent.

In table 2 the numbers of pairs of bud scales are indicated, mainly according to OGATA.

Dipteronia, (the other genus in *Aceraceae*) lacks bud scales.

2.8. THE LEAVES

For classification purposes some taxonomists preferred the large variations in leaf shape within the genus to other morphological characters. Several species derived their names from foliar characteristics e.g. *A. carpinifolium*, *A. cissifolium*, *A. macrophyllum*, *A. palmatum*, *A. pentaphyllum*. Some species were described from vegetative shoots only, e.g. *A. buergerianum* Miquel (1865), *A. discolor* Maximowicz (1880), *A. schwerinii* Pax (1892). PAX (1885) based

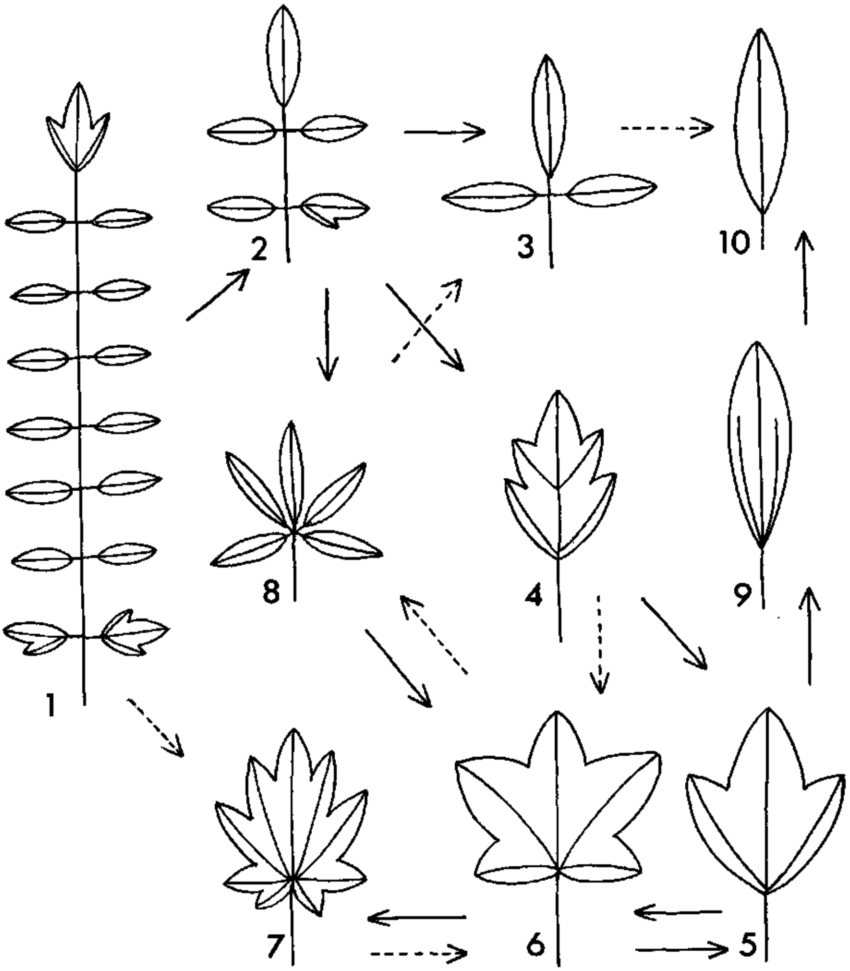


FIG. 4. Basic leaf types in *Aceraceae*: 1. pinnate (*Dipteronia*); 2. pinnate; 3. trifoliolate; 4. pinnatilobed; 5. trilobed; 6. 5-palmatilobed; 7. 7-11-palmatilobed; 8. palmatifoliolate; 9. entire, with strong basal veins; 10. entire, pinnately veined. The arrows indicate possible evolutional trends. A development as shown by the dotted arrows seems less probable in the case of *Acer*.

several sections on leaf characters, which are expressed by their designations: *Indivisa*, *Integrifolia*, *Palmata*, *Trifoliata*.

Many fossil *Acer* species were only based on their typical palmate leaf print.

However, leaf shape is a rather unreliable character. Various climatical and ecological circumstances cause wide specific and intraspecific variations in shape and texture of leaves. Leaves of juvenile plants sometimes largely differ from leaves of adult plants. Species with entire leaves can have distinctly three-lobed, juvenile leaves (e.g. *A. davidii* and *A. oblongum*). Young seedlings of trifoliolate species develop some three-lobed leaves. The first pair of leaves is unlobed except in some species with many-lobed leaves as found in series *Palmata*. In figure 4 several leaf types are shown. The distribution of these types in the genus is given in table 2. Evolutional trends of leaf shapes will be discussed in 7.3.4.

3. FLOWERING AND SEX EXPRESSION (OBSERVATIONS)

3.1. INTRODUCTION AND LITERATURE

In the course of the last two centuries a considerable number of notes on the flowering and sexuality of various *Acer* species have been published. However most students published their observations while they were not or incompletely posted on the subject by previous publications. Some papers here cited, were never mentioned in previous publications. Repeatedly published notes contradicted other publications.

Most taxonomists, who worked on the genus, e.g. KOIDZUMI (1911), POJARKOVA (1933), FANG (1939, 1966), MOMOTANI (1961) and MURRAY (1970) supplied neither special data nor cited literature in relation to the sexuality. PAX (1902) referred to WITTROCK (1886). Only SARGENT (1891, 1905) and OGATA (1965, 1967) gave some information about the sex expression of some species which they had observed.

Another consequence of the wanting knowledge of flowering and sex expression in *Acer* are the incomplete and often incorrect data in most botanical manuals.

The first data on differences in flowering can probably be attributed to LINNÉ (1742) and JUSSIEU (1789) (see footnotes on p. 16), but the first detailed notes were published by WAHLENBERG (1820). Observing the flowers of *A. platanoides* WAHLENBERG noticed that the inflorescences on some trees had only ♂ and other trees had only ♀ flowers at the beginning of anthesis, while during flowering also some flowers of the other sex were produced.

NEILREICH (1846) described the occurrence in Middle European species of trees with flowers of both sexes, but also of completely ♂ flowering specimens.

A detailed description of flowering of two *A. platanoides* trees was given by BUCHENAU (1861). The first had large inflorescences and anthesis of ♂ flowers started before the unfolding of the leaves. This stage with ♂ flowers was followed by a stage with ♀ flowers. The second tree had small inflorescences which started flowering simultaneously with the unfolding of the leaves. On this tree the sequence of the sexes was opposite: ♀ flowers followed by ♂ flowers. WITTROCK (1886) made the first extensive study of flowering in *Acer*. He studied 5 species. His main subject was an observation of the flowering of 100 street trees of *A. platanoides* at Stockholm in 1883 and the same number at Budapest in 1885. On the basis of sex expression of single inflorescences he distinguished 5 possibilities, which he called 'Infloresccenztypen'. Instead of this misleading term the present author uses the term flowering type. Completely ♀ inflorescences were type A. A phase of ♀ flowers followed by one with ♂ represened type B. The sequence ♂–♀–♂ was type C, and ♂–♀ type D. Completely ♂ inflorescences were designated as type E. (see fig. 5).

Nearly all inflorescences of a single tree belonged to the same flowering type, but sometimes two and even three flowering types were found on the same tree. Depending on the length of the female phase WITTROCK distinguished two subtypes in types B and D. The results of his observations are listed in table 3. Following CORRENS (1928) the indication of subtypes is omitted.

Regarding the high number of ♂ flowering trees (type E) at Stockholm, WITTROCK remarked that this might be due to the poor and dry soil, in which the trees were growing. A further explanation is given for the combination of type B and F (type E sensu WITTROCK). The ♂ inflorescences were very small and anthesis did not start until the inflorescences of type B finished flowering.

In the environs of Budapest WITTROCK studied the flowering of 50 specimens of *A. campestre*. The same variations were found which he observed earlier in *A. platanoides*. These results are also shown in table 3.

After his discovery of variable sex expression in *A. platanoides*, VOGLER (1906) studied the flowering of 5 trees during two seasons (see table 3). In both years four trees had the same sex expression, while the ♀ phase of tree number 5 was followed in only one year by ♂ flowers. Concerning the successions of ♂ and ♀ flowers he remarked that the change from one phase to another was about synchronous in the whole tree. As a rule flowers of the same sex flowered simultaneously.

An almost unnoticed paper is the thesis of HAAS (1933): 'Untersuchungen an der Gattung *Acer*'. He made his studies mainly on *A. platanoides*. For three years he observed the flowering of a number of street trees at Munich (see table 3). During this period nearly all the trees showed inflorescences of the same flowering type. In one year on three trees the ♀ phase was not followed by a second phase of ♂ flowers. HAAS described in detail the two types of ♂ flowers. The size of the abortive pistils of flowers of the second ♂ phase was decreasing at the end of anthesis.

WRIGHT (1953) observed the flowering of 34 trees of *A. platanoides* for 5 years. He found the same flowering types as described by WITTROCK except type A (♀ inflorescences). Only 9 trees had an unchanged sex expression during this period, among them 3 completely ♂ flowering ones. He noticed a nearly strict dichogamy, with little overlapping of the ♂ and ♀ phases. Dichogamy was rather imperfect in *A. saccharum*. WRIGHT suggested that this was due to a pronounced trend in this species towards dioeciousness. Most of the trees in the Philadelphian area (Pennsylvania, USA) produced either ♂ flowers or ♂ and a few ♀ flowers. Two of the 47 observed trees produced ♀ flowers in 3 of the 4 years. Half the number of trees did not produce ♀ flowers in the four years of observations, while the remaining trees produced ♀ flowers in one year (1950) or in that year and in another year. WRIGHT also found that there was a noticeable limitation of the ♀ flowers to certain portions of the tree crown, other branches bearing only ♂ flowers.

GABRIEL (1968) described protogynous and protandrous flowering trees of *A. saccharum*, corresponding with WITTROCK's types B resp. D. This hetero-

TABLE 3. Results of observations on the sex expression in *Acer* of various authors in terms of flowering types as shown in fig. 5.

author, species (area and year)	total number of trees	flowering types of individual trees									
		A	B	C	D	E	F	G	B+F	D+E	other combinations
WITTROCK (1886) *A. platanoides* (Stockholm, 1883)	100		47	3	24	18			1	6	1
A. platanoides (Budapest, 1885)	100	1	50	6	20	7			4	9	3
A. campestre (Budapest, 1885)	50	2[1]	21	3	8	5			3	6	2
VOGLER (1906) *A. platanoides* (St. Gallen, 1905)	8		2	5	1						
(ibid. 1906)	5		1	4[2]							
HAAS (1933) *A. platanoides* (Munich, 1930)	15		4	7	4						
ibid. (1931)	15		5	3	7[3]						
ibid. (1932)	15		5	4[4]	6[5]						
A. circinatum (Munich)	13		1	12							
SCHOLZ (1960) *A. platanoides* (Waldsieversdorf, 1958)	74	1	35	11	9	12	3	3			
A. pseudoplatanus (ibid.)	39	5	9	5	2	17		1			
GABRIEL (1968) *A. saccharum* (Vermont, 1960)	35		18		17						
SVOBODOVA (1973) *A. platanoides* (Prunochice, 1964-6)	150		36		110	4[6]					

[1] A or B; [2] one tree type D in 1905; [3] one tree type C in 1930 and 1932; [4] one tree type C in 1931; [5] one tree type C in 1930 and 1931; [6] two trees with some ♀ flowers in 1965 and 1966.

dichogamous condition was found after 'casual' observations of more than 100 additional trees in Burlington Green Mountain, Vermont (USA). Other observations of GABRIEL elsewhere in that state indicated a 1:1 ratio of these types: 18 of 35 trees sampled were of type B, 17 of type D. The sex expression of some trees was observed for 2–3 years and no variations were found. When the temperature during flowering was fairly high GABRIEL (1966) found a complete segregation of the ♂ and ♀ phases. Cold weather caused an extension of stigma receptivity of the ♀ flowers and consequently some overlapping of the ♀ and second ♂ phases.

This short chronological review of the most important papers on the sex expression of *Acer* already presents different observational results. Several other short notes on the sex expression of *Acer* species will be discussed in the corresponding sections (3.4).

3.2. MATERIALS AND METHODS

Most intensively studied was the maple collection in the Botanic Gardens of the Wageningen Agricultural University (Wag. B.G.). This collection included taxa of various rank and origin: species, varieties and cultivars grown from seeds or propagated by grafting. It consisted of more than 150 trees belonging to 35 species. The trees in the old arboretum 'De Dreyen' were planted round 1900. However most of the maples were at 'Belmonte' and had been planted in 1953 or later. Studies of this collection started in 1966. In the same period observations were also made at the 'Sortimentstuin' of the Nursery Experiment Station at Boskoop. The maple collection there consisted of cultivars of *A. japonicum* and *A. palmatum*, mainly planted in 1948.

From 1967 to 1970 near Boskoop roadside plantings of about 700 *A. pseudoplatanus* trees, grown from seeds, were studied. The trees on the northern verge were planted in 1946. South of this row there was a row in the verge between the main roadway and the cycle track planted in 1948.

In the period 1969–1971, the maple collections in the Zuiderpark at The Hague and the Gimborn Arboretum at Doorn were studied. The collections there amounted to 30 and 21 species respectively.

Studies were also made at Wageningen of street trees (*A. saccharinum*) and a few trees run wild on the 'Wageningse Berg' (*A. campestre* and *A. platanoides*). At The Hague some street trees (*A. pseudoplatanus*) were studied. Incidental studies were made at the nurseries of Alphons van der Bom at Oudenbosch (*A. pensylvanicum* and *A. rubrum*), the Arboretum Kalmthout at Kalmthout (Belg.) (several species) and the Jardin des Plantes in Paris (*A. monspessulanum* and *A. opalus*).

Outside the flowering time single studies were made in Great Britain: The Kew Botanic Gardens, the Gardens of the Royal Horticultural Society at Wisley, Winkworth Arboretum at Godalming, Jermyns Gardens & Arboretum near Winchester, Westonbirt Arboretum at Tetbury, the gardens of Caerhays Castle and Trewithen (Cornwall), Borde Hill (Sussex) and Hergetscroft (Gloucestre). In Belgium: Arboreta of Kalmthout and Tervuren and in France: Arboreta des Barres at Nogent sur Vernisson, Vilmoriensis at Verrières le Buisson and Chevreloup at Rocquencourt.

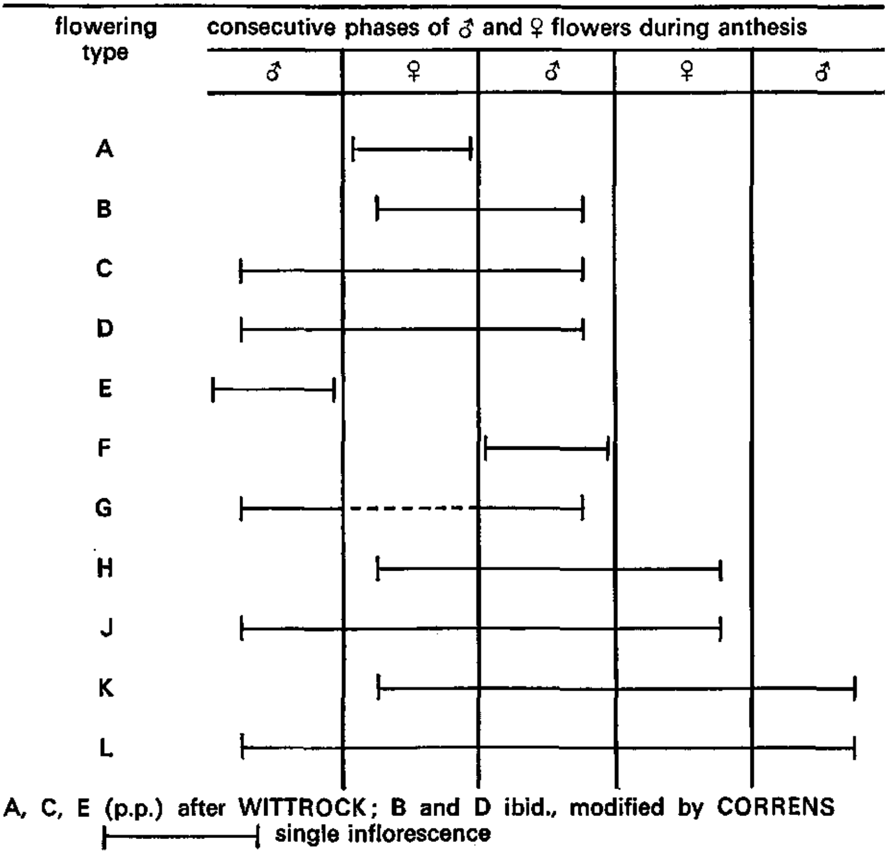
At all places mentioned above herbarium collections were made, sometimes flowers were fixied in FAA (formaline 5%, alcohol 70%, acetic acid 25%).

Flowering and sex expression were also studied on herbarium specimens.

Visits were made to the herbaria of the Royal Botanic Gardens at Kew (K), The British Museum (Natural History) at London (BM), Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie at Paris (P), Royal Botanic Garden at Edinburgh (E), the Rijksherbarium at Leiden (L), Botanical Museum and Herbarium at Utrecht (U). Loans were obtained from these herbaria and from the Naturhistorisches Museum at Vienna (W). Some material was obtained from the Arnold and University of Washington Arboreta (USA).

Observations on living material were made throughout the flowering period. At Wageningen these studies could be made almost daily. At the other places in The Netherlands mentioned above there were intervals of 7–10 days between the observations. The mode of sex expression of the inflorescences was recorded by using the classification of WITTROCK (1886) as modified by CORRENS (1928). It was necessary to increase the number of flowering types. All the variations found in sex expression are shown in fig. 5. Type F includes a part of WITTROCK's type E, viz. inflorescences with ♂ flowers of the second type as found in androgynous inflorescences after the ♀ phase.

Fig. 5. Flowering types of *Acer* inflorescences



A, C, E (p.p.) after WITTROCK; B and D ibid., modified by CORRENS

Besides records of the flowering types, studies were made of the alternation of ♂ and ♀ phases as influenced by weather conditions. Special attention was given to some trees showing a more or less irregular flowering.

In some cases, ♂ and ♀ flowers of trees or parts of trees were counted.

3.3. RESULTS OF OBSERVATIONS PER SECTION

I. Section Acer

A. Series Acer

1. *Introduction and literature*

Acer pseudoplatanus was by far the most studied species of this series. Only a few trees of *A. trautvetteri* and *A. heldreichii* were available. The remaining species were mainly studied from herbarium specimens. Besides observations in the Botanical Gardens at Wageningen, special visits were made to roadside *A. pseudoplatanus* near Boskoop. Data were collected on the variation in flowering types from a large number of specimens of the same species; the relations between flowering type, the first date of anthesis, frequency of flowering and size of the trees (see par. 4).

Although no data were reviewed in 3.1 the earliest papers gave some information on the sex expression of *A. pseudoplatanus.* BUCHENAU (1861) supposed that this species flowered in the same way as *Acer platanoides*, and that protandrous trees predominated. This was also observed by HAAS (1933 in Bayer and by KLAEHN (1959), but they too did not give detailed information.

MAC LEOD (1894) reported that the flowering of *A. ps.* could start with either ♂ or ♀ flowers. In a later stage of flowering probably always flowers of the other sex appeared, for no entirely ♂ or ♀ inflorescences were found. On a single tree all the inflorescences had the same variation in sex expression. He further described the two types of ♂ flowers (see 3.2). WITTROCK (1886) and HAAS (1933) mentioned the occurrence of ♂ and ♀ terminal flowers on the main axis of *A. ps.* inflorescences after flowering started with ♀ flowers (see par. 9).

SCHOLZ (1960) studied the flowering of 39 trees of *A. ps.* near Berlin. He distinguished 7 variations in mode of flowering in accordance with floral morphology. The detailed descriptions of these flowers enables the present author to determine the corresponding flowering types (see table 3). The main subject of his study was to examine if ♂ (flowering) specimens grew faster than monoecious specimens. Of the latter he only took the protogynous ones. He found a mean variation of about 5 per cent in height and of 20 per cent in stem diameter. But he also noticed that most of the ♂ flowering specimens had produced fruits in the previous year.

WEISER (1973) made some quantitative analyses of the sex expression in *A. ps.* He found that ♂ and protogynous inflorescences had about 20 percent less flowers than protandrous ones. The average portion of ♀ flowers of androgynous inflorescences was about 15 percent. With protandrous inflorescences, and

FIG. 6. *Acer pseudoplatanus* L.: Duodichogamy (flowering type C): 1. flowering branchlet with infl. at the end of the ♂$_{\mathrm{I}}$ phase (May 22, 1969) (1 ×); 2. infl. during ♂$_{\mathrm{II}}$ phase (June 3, 1969) (1 ×). Wag. B.G. no. 11480).

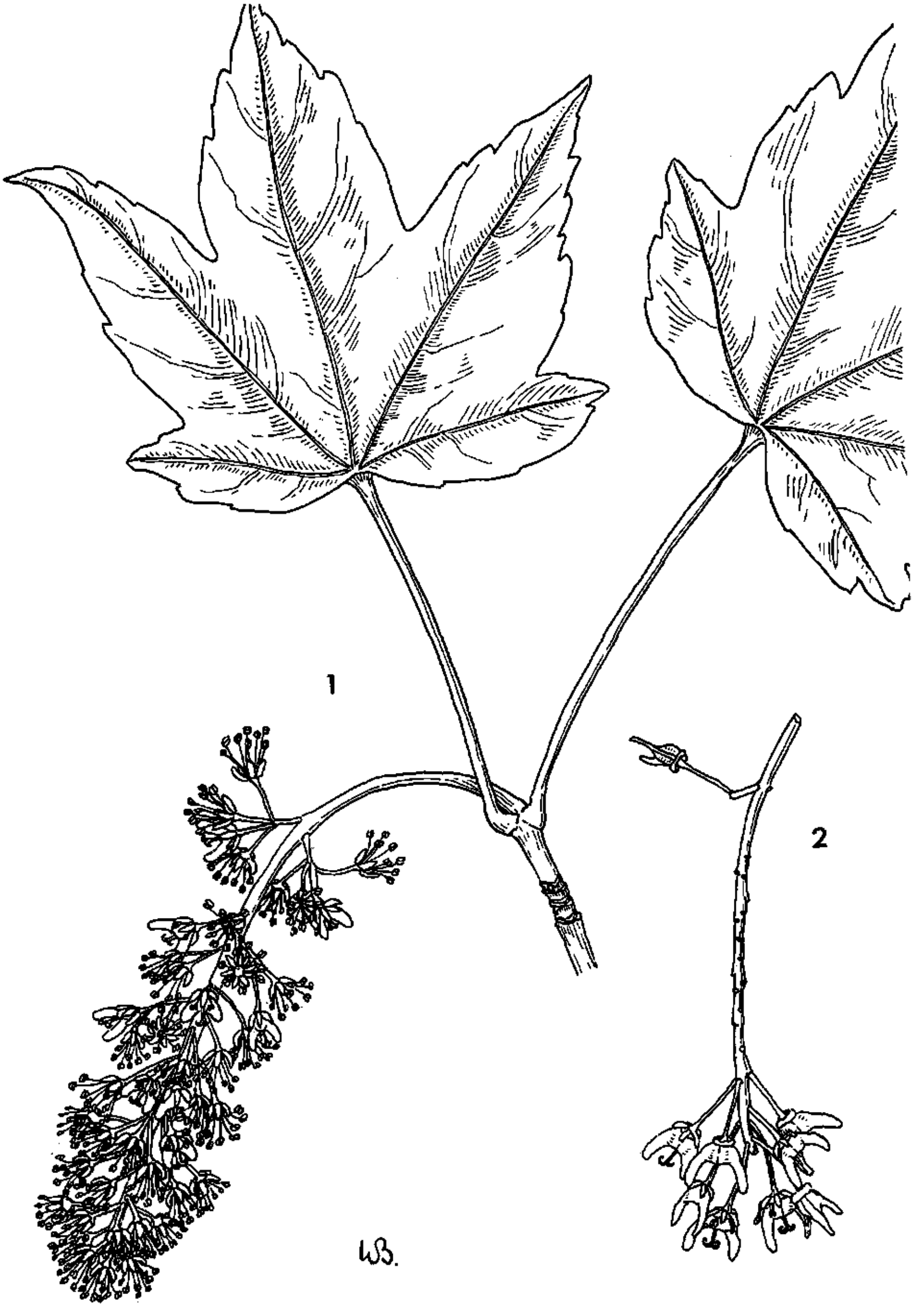


FIG. 7. *Acer pseudoplatanus* L.: 1. protogynous infl. (flowering type B) during ♂$_{\text{II}}$ phase (June 4, 1969 (1 ×); 2. protandrous infl. (flowering type D), ♂$_{\text{I}}$ fl. dropped (May 28, 1969) (1 ×). (Wag. B.G. no. 11480).

sometimes with ♂ inflorescences WEISER noticed the occurrence of asexual flowers, which partly drop before anthesis. On the same inflorescences he further distinguished flowers with an unexplained sexuality. The present author holds the view that they are ♂$_{\mathrm{II}}$ flowers because ♂$_{\mathrm{II}}$ flowers were only described in the case of protogynous inflorescences.

2. *General observations on flowering*

The mixed buds of *A. ps.* were opening at an earlier stage than leafy buds. Depending on the weather conditions and the precocity of single trees, mixed buds were bursting between mid April and mid May. The divergence in time of unfolding of mixed and leafy buds depended mainly on the weather conditions and was nearly absent during relatively warm weather. In rather cold weather the inflorescences remained very compact and flowering could start before the unfolding of the leaves. The flowering period in The Netherlands was from the last week in April till the middle of June. For a single tree the duration of flowering was 2.5–6 weeks.

At the moment of bursting of the mixed buds the sex differentiation in ♂$_{\mathrm{I}}$ had already taken place, but not the differentiation in ♂$_{\mathrm{II}}$. The inflorescences of *A. ps.* are somewhat deviating from those of the other species in the series *Acer* (see (2.3.1). They have an elongated main axis. The terminal flower of this axis is not the first to open. The basal structure of the inflorescences is cymous. The last formed parts, however, are almost completely racemose. The first flowers appeared from the terminal buds of the lowest secondary axes. The number of flowers of an inflorescence varied from 25 to 150. Within an inflorescence ♂$_{\mathrm{I}}$ and ♀ flowers did not flower at the same time. Between the ♀ phase and the ♂$_{\mathrm{II}}$ phase some overlapping was possible. This depended on the duration of the receptive period, which was lengthened by relative cold weather conditions during flowering of the ♀ phase. Figure 6, 7 and 8 show flowers and inflorescences of *A. ps.* Some special observations are described in the following paragraphs.

3. *Variation in flowering types*

Table 4 gives the combined results of 6 years of obervations in the Wag. B.G. If more than one flowering type was found on a single tree, they were arranged in order of frequency. The results of 1966, the first year of observations, are probably not quite correct owing to still insufficienct proficiency at that time.

The trees rarely failed to flower in one of those years. The gaps in the table are caused by young trees which failed to flower in the first few years of observation and by trees cut down during this period.

The trees which produced ♀ flowers first were very stable. The yearly variations of trees with a ♂$_{\mathrm{I}}$ phase were mainly due to a variable duration of this ♂$_{\mathrm{I}}$ phase and a variable number of flowers per inflorescence.

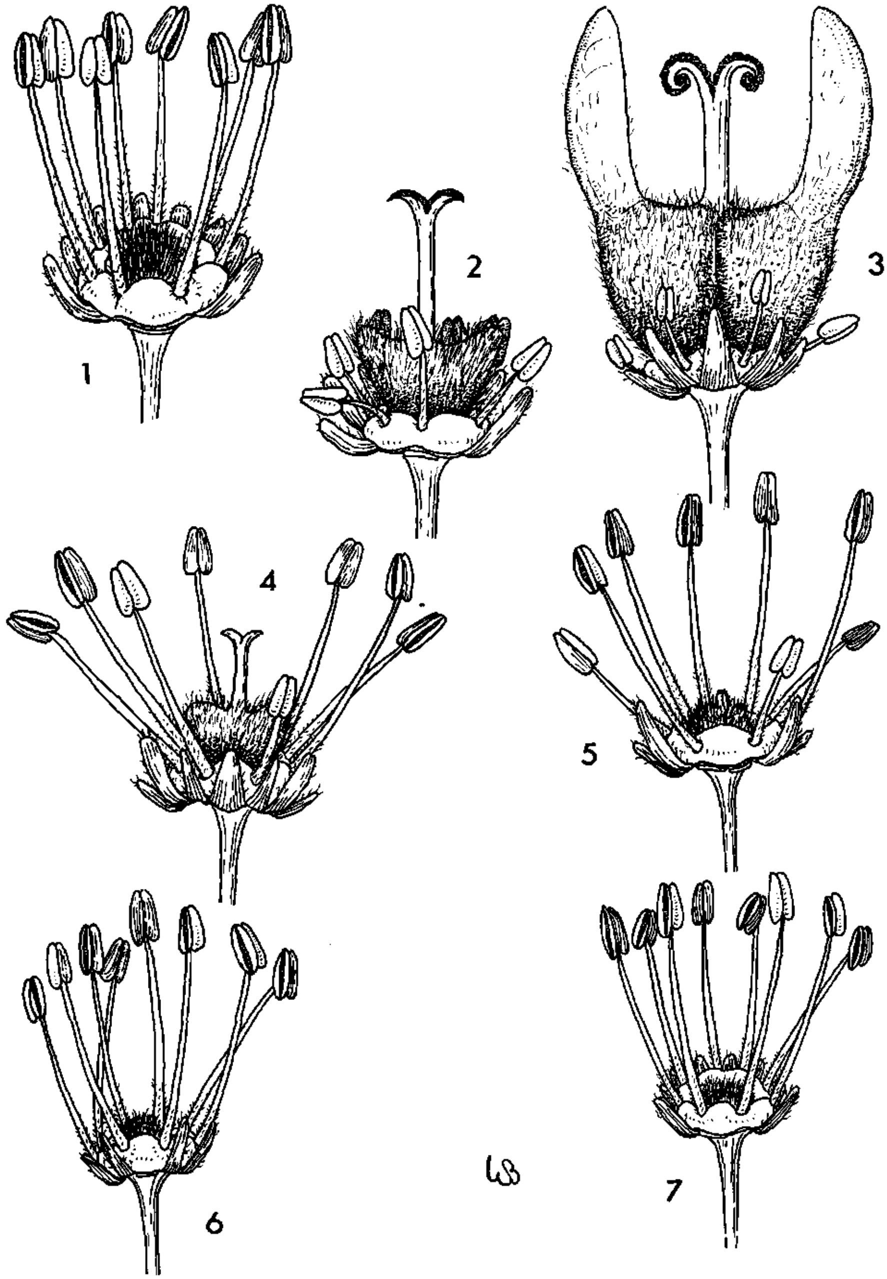


FIG. 8. *Acer pseudoplatanus* L.: Flowers (5×): 1. ♂$_{\text{I}}$ fl, 2. ♀ fl. at the beginning of anthesis, 3. ♀ fl. near the end of the receptive period, 4–7. ♂$_{\text{II}}$ fl. produced at various times during the ♂$_{\text{II}}$ phase showing decrease in pistil development and size of the fl. (Wag. B.G. no. 11480).

TABLE 4. Flowering types observed on specimens of series *Acer* between 1966 and 1971 in the Wageningen Botanic Gardens.

species cultivar	garden number	flowering types (in order of frequency)					
		1966	1967	1968	1969	1970	1971
A. heldreichii	12279	B	B	B	B	B	B
A. pseudoplatanus	7191	D	D	D,E	D	D,C,B,	D,C
	8385	B	B	B	B	B	B
	11468	D	D,C	C,D	C,D	D,C	C,D
	17717	–	–	C,D	D,C,B	C,D,B	C,D
	11480	D,B	D,C	C,B,D	C,D,B	D,C,B	C,D,B,A
'Atropurpureum'	11714	D	D,E	D,C	J,D,K	D,C	D,C
'Atropurpureum'	11714	–	D,E	+			
'Costorphinense'	8382	B	B	B	B	B	B,C
'Digitatum'	17716	–	–	B	B	+	
'Erectum'	12287	D	D	D,C	C,D	C,D	C
'Fastigiatum'	12286	E	E	+			
'Leopoldii'	11460	B	B	B	B	B,F	B
'Negenia'	17651	–	–	B	–	B	B
'Nervosum'	17859	–	–	B	B	B	B
'Prinz Handjery'	11356	B	B	B	B	B	B
'Prinz Handjery'	12117	B	B	B	B	B,F	B
'Purpureum'	11474	B	B	+			
'Purpureum'	11464	B	B	B	B	B	B
'Serotinum'	17715	–	–	C,D	D,C	C,D	D,C
'Simon Louis Frères'	12483	–	–	D,E	D	D,C	D
'Variegatum'	12118	D	D,E	D,C	D,C,E	C,D,E	D,C
'Worleei'	11475	–	B	B	B	B	B
'Zenith'	17562	E	E	D,E	E,D,C	E,D,B	E,D
A. trautvetteri	10883	–	–	–	C	C	C
	11976	–	–	–	B	B	B

– no flowers + cut down

4. *Studies on a roadside planting near Boskoop*

After an observation period of 4 years the results of 626 trees were worked out. Trees planted later than 1948 or cut down during the observational period have not been taken into consideration. The following subjects were studied:

a. The flowering types and the frequency of flowering
b. The dates at which flowering started on the individual trees.
c. The size of the trees (estimated in 1970).

In accordance with the observed flowering types the trees were divided into two groups. The first included specimens starting anthesis with ♂ flowers while the second group consisted of trees starting predominantly ♀ (see table 5).

The dates on which anthesis started in 1968 and 1970 were used to study the relation between these dates and the flowering type. The period in which anthesis started, was divided into 5 parts of about 6 days each: very early, early, midseason, late, very late. If trees failed to flower in one of these years, the dates of the remaining year were used. The 4 trees, which did not flower in both years

TABLE 5. Some results of observations on a road plantation of *A. pseudoplatanus* near Boskoop between 1967 and 1970.

		duodichogamous, protrandrous and ♂ flowering trees		(predominantly) protogynous trees		trees not flowering	
		number	% of all trees in this category (351)	number	% of all trees in this category (265)	number	% of total number of trees (626)
years of observation	1967	282	80	215	81	129	21
	1968	339	97	255	96	32	5
	1969	155	44	128	48	343	55
	1970	342	97	258	97	26	4
frequency of flowering	all years	140	40	120	45		
	3 years out of 4	144	41	97	377		
	2 years out of 4	55	16	37	14		
	1 year out of 4	12	3	11	4		
	not flowering					10	2
start of anthesis	very early	36	10	12	4		
	early	93	27	54	20		
	midseason	92	26	47	18		
	late	81	23	91	34		
	very late	49	14	61	23		
relative size of the trees	large	205	58	147	56	1	
	medium	100	29	75	28	6	
	small	46	13	43	16	3	
total number of trees (626)			% of 626		% of 626		
		351	56	**265**	42	**10**	2

were disregarded. The first release of pollen and the moment when receptivity of the stigmas began, were considered as the beginning of anthesis.

In 1970 a rough division was made into tall, medium and small trees. Both the thickness of the stem and the width of the crown were taken into account.

Table 5 shows some results. There were 351 trees with a ♂$_I$ phase (56% of all trees), while 265 trees (42%) started flowering predominantly with ♀ flowers. Ten trees (2%), including one large tree, failed to flower in this period. In two years, 1968 and 1970, nearly all the trees flowered; in 1969 less than 50 per cent of all trees under observation flowered while several of the flowering specimens produced only few inflorescences. There was no relation between the frequency of flowering and flowering type. i.e. a ♂ or ♀ start.

It may be concluded from the results that some relation exists between the date when anthesis started and the sex of the first phase of flowers. Trees with a ♂$_I$ phase had a mean precocity of about 2.3 days. There was hardly any relation between the size of the trees and the two groups of flowering types. Some other aspects of flowering in this plantation will be discussed in the next paragraphs.

5. *Stability of protogynous flowering*

At Wageningen $♂_{\mathrm{I}}$ flowers were observed only once on a tree with flowering type B. In 1971 *A. ps.* 'Costorphinense' (no. 8382) had some rather small inflorescences of type C. By contrast in the road plantation near Boskoop this variation was found during all years of observations. A number of 37 trees showed this deviation in one year and 4 trees in two years, which means 15.8 per cent of all protogynous trees.

The few $♂_{\mathrm{I}}$ flowers were mainly present on some inflorescences in the lower parts of the crown at the south or east sides of the trees. All these trees had a relatively early start of anthesis. The stability of a ♀ onset of flowering seemed to be slightly affected by environmental conditions, but no relation to the length of the $♂_{\mathrm{I}}$ phase on trees with a ♂ start of flowering could be shown.

6. *Annual variations in trees with a $♂_{\mathrm{I}}$ phase*

From table 4 it can be seen that protandrous trees showed annual variations in their flowering types. These variations were calculated for those trees near Boskoop with a $♂_{\mathrm{I}}$ phase which flowered in 1968, 1969 and 1970. (See table 6). The flowering types of 143 trees were arranged according to dominating flowering types C, D or E. Besides the number of each flowering type or combination of types the shift with regard to the results of 1968 is also indicated.

The table clearly shows a higher number of dominating types D and E in 1969, which must be mainly attributed to an increase in the number of $♂_{\mathrm{I}}$

TABLE 6. Annual variations in the portion of $♂_{\mathrm{I}}$ flowers on proterandrous flowering trees of a road plantation of *A. pseudoplatanus* near Boskoop between 1968 and 1970.

groups of predominant flowering types with subgroups with increasing portion of $♂_{\mathrm{I}}$ flowers	number of trees								
	1968	1969				1970			
	per group and subgroup	per group and subgroup	predominant types of the group in 1968			per group and subgroup	predominant types of the group in 1968		
			C	D	E		C	D	E
C	**94**	**56**	45	10	1	**108**	82	23	3
C,B	8	4				4			
C	60	37				54			
C,D	23	14				40			
C,D,E	3	1				10			
D	**39**	**59**	42	15	2	**24**	10	11	3
D,C	16	6				8			
D	13	48				13			
D,E	10	5				3			
E	**10**	**28**	7	14	7	**11**	2	5	4
E,D	7	16				5			
E	3	12				6			

flowers per inflorescence and partly to a decrease in the total number of flowers per inflorescence.

From this table it also appears that despite this general tendency in 1969, 13 trees (9 %) showed a trend in the opposite direction. Comparison of the results of 1968 and 1970, which are rather similar for the numbers of each flowering type, still gives a shift for 29 trees in one and 17 trees in the opposite direction.

7. *Variations in the number of ♀ flowers per inflorescence*

Many limiting factors regulate the number of ♀ flowers in an inflorescence. In general, on one tree, big inflorescences of types B or C have more ♀ flowers than small ones. Inflorescences on the periphery of the tree crown usually carry more ♀ flowers than those further inside. In type D the number of ♀ flowers will be limited by the number of flower buds that remain after the ♂$_{\text{I}}$ phase.

Individual trees also show variation in the duration of the ♀ phase, e.g. *A. ps.* 'Worleei' (no. 11475) and 'Leopoldii' (no. 11460) had a low average number while 'Costorphinense' (no. 8382) and trees nos. 8385, 11480, and 17717 of the Wag. B.G. had about a double number of ♀ flowers each year.

Environmental conditions caused yearly variations in the duration of the ♀ phase. The average numbers of ♀ flowers of 'Leopoldii' (no. 11460) between 1968 and 1971 were: 7.5, 4.5, 4.4 and 5.6. Although annual variations in the average size of the inflorescences occur, it was established that the largest inflorescences of 1967 and 1968 had 15 and 8 ♀ flowers respectively, although they were of equal size.

Temperature appeared to be a regulating factor for the determination of the borderline between the ♀ and ♂$_{\text{II}}$ phases. Moderate and low temperatures retarded sex differentiation of the ☿ buds, which led to further development of the pistil and an increase in the number of ♀ flowers. A possible cause could be less competition of the ♀ buds and flowers. This competition affected the development of the pistils of the ☿ flower buds (see 5.4). Consecutive days with temperatures above 20 °C shortly before the appearance of the ♀ flowers, or at the beginning of the ♀ phase, limited the number of ♀ flowers.

A very late differentiation into ♂$_{\text{II}}$ flowers was observed in 1968 on 4 trees: *A. ps.* 'Erectum' (no. 12287) and trees nos. 11468, 11480 and 17717. After the ♀ phase these trees had some flowers with a parthenocarpic development of the ovaries, and especially of the wings. Yet they functioned as ♂ flowers. However, sometimes only part of the stamens released pollen. The development of the style and ovules lagged behind (see fig. 9, 4–6). The parthenocarpic development still continued after the differentiation into ♂$_{\text{II}}$ flowers, but the 'fruits' dropped soon after flowering.

An analysis of the temperature range before the appearance of these abnormal flowers showed a period of low day temperatures (below 15 °C) between the 17th and 23th of May, followed by a period with day temperatures between 15° and 23 °C. This last period started a few days before the appearance of the ♀ flowers on these 4 trees.

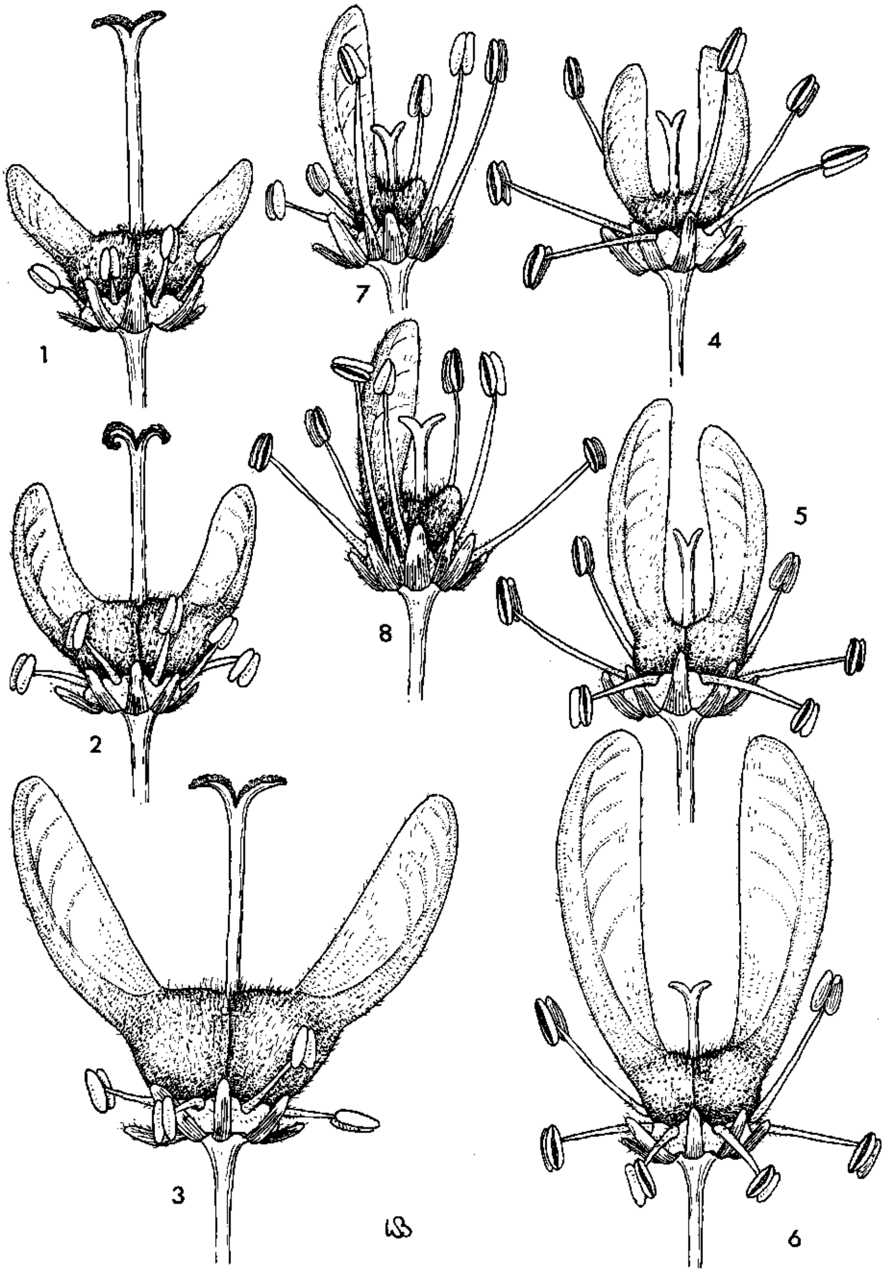


FIG. 9. *Acer pseudoplatanus* L.: 1–3. ♀ fl. at various times during anthesis (4×); 4–6. functional ♂$_{\text{II}}$ fl. showing strong pistil development: in comparison with the ♀ fl. the development of ovary, style and stigmas lag behind and wing development continues (4×); 7–8. ibid.: only one wing developed (4×). ('Erectum' Wag. B.G. no. 12287).

Some of these abnormal ♂$_{II}$ flowers had only one developed wing (see fig. 9, 7–8). This abnormality was observed several times, particularly on the trees near Boskoop. In all cases they formed the borderline between the ♀ and ♂$_{II}$ phases, but pollen shed was retarded (see also II *Plat* par. 9).

8. *Occurrence of a second ♀ phase.*

The first records of inflorescences with a second ♀ phase were made in 1968 at The Hague. Very occasionally, on the 15th of June in the Prins Mauritslaan 3 seedling trees of *A. ps.* with some inflorescences of 'type H' were found. These trees probably flowered for more than 5 weeks. The inflorescences of type H were rather large, the main axis being up to 25 cm in length. The fruits of the first ♀ phase had already wings of up to 3 cm. The ♀ flowers of the second ♀ phase were mainly situated near the top of the main axis and sometimes on the lowest secondary axes of the inflorescences.

In 1969 the same phenomenon was found at Wageningen at the end of May on two trees of *A. ps.*: nos. 11480 and 17717. The second ♀ phase appeared mainly on some of the largest inflorescences and was usually at the top of the main axis. Sometimes the second ♀ phase was followed again by ♂ flowers. So the flowering types of these inflorescences were J. and K. See figure 10, 1–3. Because so many trees of this species were studied for 4 to 6 years, this phenomenon must be very exceptional and due to a coincidence of special environmental conditions. A second ♀ phase could also be obtained experimentally: see 5.4.3.

From these experiments a strong competition was observed between the ♀ flower buds or flowers and the undifferentiated flower buds. This competition caused an abortion of the ovaries and consequently a differentiation into ♂$_{II}$ flowers. In case of a second ♀ phase, the competitive power of the ♀ buds and flowers on some undifferentiated buds, probably was so small that the development of the pistils of these buds was not affected and ♀ flowers could arise.

The weather conditions during flowering in 1969 were rather exceptional. Between 27 April and 5 May maximum temperatures varied between 15° and 18 °C except on 2 May (12 °C). Anthesis started at the end of this period. This period was followed by a spell of rather cold weather. Ecxept on two days temperatures of 15 °C were not recorded. These low temperatures may have reduced the competitive effects.

9. *Variations in the sex expression of the terminal flowers*

Some notes in literature deal with the sex expression of the terminal flowers on the main axis of *A. ps.* inflorescences. Wittrock (1886) described a specimen with flowering type B, with ♂ and ♀ terminal flowers. The type D specimen had only ♂ terminal flowers. Mac Leod (1894) reported that the terminal flowers rather occasionally were ♂. The observations of Haas (1933) agreed with those of Wittrock. Weiser (1973) found that on protogynous specimens about 25 per cent of the terminal flowers were ♀ and on protandrous specimens about 9 per cent.

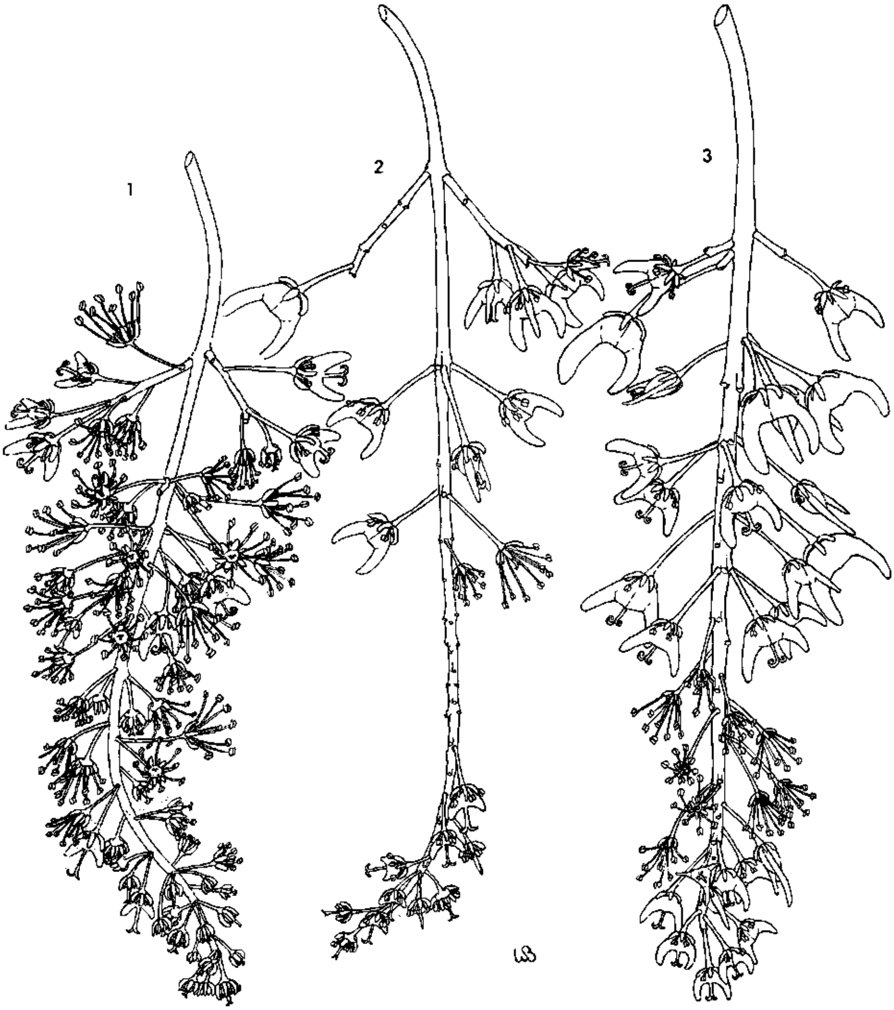


FIG. 10. *Acer pseudoplatanus* L.: 1–3. infl. with a second phase of ♀ fl. (1 ×): 1. ♀ fl. buds visible (mainly) near the top of the rachis (May 29, 1969), 2. full anthesis of second ♀ phase (June 6, 1969), 3. continuous development of $♂_{II}$ fl. in the middle of the rachis (June 9, 1969). (Wag. B.G. no. 11480).

The present author noticed that nearly all protandrous and most of the protogynous trees had only ♂ terminal flowers. Special observations were made on 'Prinz Handjery' (no. 11356), a protogynous cultivar with ♂ and ♀ terminal flowers. Depending on the length of the main axis of the inflorescence the terminal flower opened earlier or later during flowering, which meant anthesis during the ♀ phase or later. Besides a variation in the size of the inflorescences the number of ♀ flowers per inflorescence was important for the occurrence of ♀ terminal flowers (see par. 7).

In 1969 some counts were made on inflorescences on the periphery and inside of the tree. Large inflorescences from the periphery of the crown had 11–16 ♀ flowers and ♂ terminal flowers. The small inflorescences on this part of the crown had 5–13 ♀ flowers and mostly a ♀ terminal flower.

The largest inflorescences from the interior of the crown had the same mean size as the small ones from the periphery of the crown. They carried 3–7 ♀ flowers and a small number of them had a ♀ terminal flower. The remaining small inflorescences inside the tree had 1–3 ♀ flowers including the ♀ terminal flower. It may be concluded that the occurrence of ♀ terminal flowers is favoured by trees with rather small inflorescences and a relatively high number of ♀ flowers per inflorescence.

In 1970 both the average number of ♀ flowers per inflorescence and the number of ♀ terminal flowers were substantially lower than in 1969.

10. *Clonal varieties and rootstocks*

Clonal varieties of *A. ps.* had the same flowering types. No influence was observed of the seedling rootstocks on which they were grafted. The two specimens of 'Atropurpureum' (no. 11714) not only opened their first flowers simultaneously, but also showed a shift to the ♀ phase on the same day. Several specimens of 'Prinz Handjery' observed elsewhere always had protogynous inflorescences. The original figure of LEMAIRE (1964) of 'Leopoldii' shows a protogynous inflorescence, which is still present on the specimens considered as typical. The observed specimens of 'Costorphinense' including the orginal tree at Costorphine (near Edinburgh) were all protogynous.

11. *Flowering on one-year-old, long shoots*

Most young trees sometimes flowered on one-year-old, long shoots, especially in years with a heavy bloom. The inflorescences on these shoots appeared both terminally and laterally and started flowering about 3–5 days later than inflorescences on other shoots of the tree. Anthesis of lateral inflorescences in its turn was some days later than that of the terminal inflorescences. In addition to these variations in the start of flowering the inflorescences of long shoots might also reach the phase with flowers of the other sex some days later.

In 1970 'Variegatum' (no. 12118) had many flowering long shoots. The inflorescences started anthesis 3–4 days later and the shift from ♂$_{\mathrm{I}}$ to ♀ was 1–2 days later than for other inflorescences of the tree. The lateral inflorescences had an average number of 55 flowers and flowering types D, C and sometimes E. The terminal inflorescences were all of type C, and had a mean number of 129 flowers. The remaining inflorescences had on average 60 flowers and types D, E and sometimes C.

'Zenith' (no. 17652) and tree no. 7191 borne on the 29th of May, 1970 one very late protogynous flowering inflorescence on a long shoot. At that time 'Zenith' was already out of flower (♂$_{\mathrm{I}}$ inflorescences) and no. 7191 still had some inflorescences in the ♂$_{\mathrm{II}}$ phase. The dwarfy cv. 'Prinz Handjery' often flowered on long shoots of the previous year. The start of anthesis on these long shoots was 8–14 days later than on other shoots. The shift from ♀ to ♂ of this protogynous specimen also showed large variations. The earliest flowering inflorescences were already out of flower, when the latest flowering inflorescences started anthesis. It was observed one month before the bursting of the mixed buds that the small leafy buds on the normal shoots were larger than the mixed lateral buds on the long shoots of the previous year. These lateral inflorescences sometimes appeared from leafless buds or were accompanied by one pair of leaves (see also 4.2).

12. *A very heterogeneous flowering tree*

The mode of flowering of tree no. 11480 presented many perplexing problems to the author. Anthesis started on the periphery of the crown in inflorescences from mixed buds with two pairs of leaves. The flowering types were C and D. More inside the tree the inflorescences appeared a few to several days later. They were smaller and had one pair of leaves. Sometimes they even emerged from leafless terminal buds. Depending on the size of these inflorescences and the date on which flowering started, they represented the flowering types C, D, B and occasionally A. This last type had very small inflorescences, which started flowering very late. Types B, C and D of this tree are shown in fig. 6 and 7. The freedom of flowering and the high number of fruits produced every year caused a poor vegetative growth and even premature death of small branches inside the crown. So the tree showed long bare branches with hardly any foliage inside the crown.

A possible explanation for this strong variability will be given later (see 5.7).

13. *Absence of a ♀ phase*

Most of the ♂ flowering specimens flowered monoeciously in at least one year of the observational period. Only two trees near Boskoop always had ♂ flowers.

It was occasionally observed that some of the last flowers of ♂ flowering specimens had large abortive pistils such as are found in $♂_{II}$ flowers. Inflorescences with only these two types of ♂ flowers represent type G.

This flowering type was also observed on monoecious specimens. In 1970 four trees near Boskoop with inflorescences of type C bore some inflorescences of normal size in which ♀ flowers were lacking. This flowering type was also obtained by forcing detached branches into flower (see 5.2.3).

14. *Degree of variability with in the series*

A study of herbarium specimens of the remaining species of series *Acer* showed that within all species the flowering types B, C, D and E occurred. Male specimens may occasionally be present. The observations on *A. ps.* showed that most populations probably have a majority of trees which start anthesis with ♂ flowers.

The fixation of a start of flowering with ♀ flowers appeared to be incomplete in *A. ps.*

B. Series Monspessulana

Two species of this series, *A. monspessulanum* and *A. opalus*, were studied from living specimens from the Wag. B.G., Kalmthout Arb. and the Jardin des Plantes in Paris.

In literature the species are described as monoecious. Haas (1933) observed 2 protandrous *A. monspessulanum* trees in the Botanic Garden of Munich. Both showed a strong segregation of the ♂$_{\mathrm{I}}$ and ♀ phases. Beskarajnaja (1971) described a ♂ flowering *A. monspessulanum* which produced some fruits in one year of the observational period.

The flowering clearly indicated a development towards wind pollination. The inflorescences, which were developed from mixed buds, started anthesis before the unfolding of the leaves. The drooping flowers had long pedicels and a perianth, which remained rather closed, as shown by blown (♂) flowers of e.g. *A. pseudoplatanus*. The ♀ flowers had large twisted stigmas. At Wageningen *A. opalus* no. 2863 flowered ♂ in all observational years, while *A. opalus* no. 12999 and *A. monspessulanum* no. 12280 were protogynous (type B). In 1970 two protogynous specimens of the latter species were observed at Kalmthout. These also had some small inflorescences with ♂$_{\mathrm{II}}$ flowers. In 1971 in Paris three old trees of *A. monspessulanum* were studied just at the start of anthesis. Two trees had ♂$_{\mathrm{I}}$ flowers and old fruit stalks of previous years. The third tree and the single specimen of *A. opalus* had inflorescences of type B.

The degree of variability in the series, and especially in both species mentioned above was further examined on herbarium specimens. Besides ♂ and protogynous specimens a few protandrous specimens were found. The portion of (genetic) ♂ specimens seems substantial, at least for *A. opalus* (see further 5.2.3).

C. Series Saccharodendron

1. *Introduction and literature*

The single species of this series *A. saccharum*, is rather rarely cultivated in The Netherlands. Only two specimens could be studied in the Wag. B.G.

The literature concerning the sex expression of this species has already been partly mentioned in 3.1 reviewing papers of Wright (1953) and Gabriel (1968). Earlier Sargent (1891) reported that the inflorescences developed from mixed terminal buds and from leafless lateral buds. The ♂ and ♀ flowers were in separate inflorescences on the same or on different trees, the ♀ flowers on terminal and the ♂ usually on lateral inflorescences.

In a previous paper Gabriel (1962) remarked that the ♀ flowers of protogynous specimens flowered 5–6 days earlier than the ♀ flowers of protandrous specimens. Gabriel (1967) further described the variation between protandrous trees at Williamstown and Burlington (Vermont, USA). On the trees at the first location the ♀ flowers appeared only in the upper parts of the crown, while at Burlington both sexes were uniformly distributed over the entire crown. The observations of Hall (1967) agreed with those of Gabriel: rhythmic flowering with protogynous and protandrous specimens.

2. *Results of observations*

The flowering time at Wageningen was about mid May. The inflorescences appeared from mixed terminal buds and also from mixed and leafless lateral buds. Anthesis started before the unfolding of the leaves. The inflorescences were upright with the flowers on long drooping pedicels showing a tendency to wind pollination.

The approximately 60-years-old trees flowered only three times during 9 years of observation, 1968, 1970 and 1974, both with protogynous inflorescences (type B). The inflorescences were mainly located in the upper part of the crown. The climatic conditions in The Netherlands are probably unfavourable for flower induction. The summers preceding these three years were relatively warm.

3. *Degree of variability within the series*

The contradictory records of GABRIEL and WRIGHT prompted a study of sex expression of herbarium specimens collected in natural habitats. They showed the flowering types B. C, D, E and F. The inflorescences showed large variations in the number of flowers. Especially small inflorescences represented the flowering types E and F.

A large influence of environmental conditions seems probable. The local and yearly variation in the sex expression may be partly due to a variation in the size of the inflorescences. Some populations may also show a slight tendency to dioeciousness through the presence of (genetically) ♂ specimens. The observed flowers of ♂ flowering specimens, however, always had very distinct ovaries with short styles, a very improbable condition for real ♂ specimens.

II. Section Platanoidea

A. Series Platanoidea

1. *Introduction and literature*

The most studied species of this series were *A. platanoides* and *A. campestre.* A study could also be made of some living specimens of *A. amplum, A. cappadocicum, A. lobelii, A. miyabei, A. mono* and *A. truncatum.*

Some special observations are described in separate paragraphs. A rather detailed analysis is made of flowering of some specimens, which flowered partly on long shoots of the previous year or which showed large annual variations.

The most important papers dealing with variations in the sex expression in *Acer* concerned *A. platanoides.*

In the first paragraph of this chapter the contributions of WAHLENBERG (1820), BUCHENAU (1861), WITTROCK (1886), VOGLER (1906), HAAS (1933) and WRIGHT (1953) were already mentioned.

In addition to *A. pseudoplatanus* the studies of SCHOLZ (1960) dealt with *A. platanoides.* As with the former species the results are interpreted by the present author in table 3. SCHOLZ found between ♂ and protogynous flowering specimens a mean variation of about 10 per cent in height and of about 20 per

FIG. 11. *Acer platanoides* L.: Protandrous flowering specimen: 1. branchlet with infl. during ♂$_1$ phase (April 28, 1969) ($^3/_4$×); 2. branchlet during ♀ phase, at right ♂ infl. out of flower (May 8, 1969) ($^3/_4$×); 3. ♂$_1$ fl. (4×); 4. ♀ fl. (4×); 5. identification of protandry (flowering type D) from old fruit stalks: scar of dropped terminal ♂$_1$ fl. and ring-shaped scar of bract (right) (4×). ('Almira' Wag. B.G. no. 14858).

cent in stem diameter. But he also noticed that 11 out of 12 ♂ flowering trees had produced fruits in the previous year.

Svobodova (1973) observed 150 trees of *A. platanoides* at Pruhonice of which 110 were protandrous and 36 protogynous. The four remaining trees flowered ♂ in 1964, while two of them produced some ♀ flowers in 1965 and 1966. Normally the ♂ and ♀ flowers of a tree did not flower simultaneously and did not change their ratios during the years of observations.

Some other papers dealing with a variable sex expression in *A. platanoides* but without new data were published by Stout (1929, Klaehn (1959), Hall (1967), Beskaravajna (1971) and Svobodova (1972).

Ogata (1967) reported on a ♂ flowering *A. mono* specimen, which was fruiting in a previous year. Wright (1953) noticed one specimen each of *A. mayrii* and *A. cappadocicum*, which flowered heavily ♂ each year.

2. *Some general observations on flowering*

The earliest flowering species of the species studied was *A. mono*. Trees were flowering at the beginning of April before the unfolding of the leaves. *A. platanoides* started anthesis about one week later. The remaing species observed started flowering at least some days after *A. plat.*, partially overlapping the flowering period of *A. plat.* in most years. Depending on the weather conditions the leaves were unfolding later or earlier during anthesis. High temperatures and a relatively late date of first flowering caused a relatively earlier unfolding of the leaves during the flowering period.

The inflorescences appeared from mixed terminal buds with 1–3 pairs of leaves. Long shoots of the previous year could also have lateral inflorescences, mostly accompanied by one pair of leaves.

The first flower to open was the terminal flower of the main axis, followed by the terminal flowers of the lowest secondary axes. Flowering sometimes started on these secondary axes, when there was a rather long rachis. The opening of the flower buds took place in groups. This was caused by the cymous structure of the inflorescences and the sex expression of the flowers. These groups never had flowers of both sexes. If a single inflorescence had a phase of ♂ flowers followed by one with ♀ flowers an overlap was never observed.

The blown ♂ flowers closed or already dropped when the ♀ flowers appeared. Small overlaps between the ♀ and ♂$_{II}$ phase were possible. This depended on the duration of sigmatic receptivity, which could be lengthened till about 6 days by relatively low temperatures. Such low temperatures also retarded the anthesis of the ♂$_{II}$ flowers.

The inflorescences of a single tree could represent a very high degree of harmonious flowering. In such a case all inflorescences started flowering on almost the same day and also the phases of ♂ or ♀ flowers appeared simultaneously. These simultaneous shifts led to a variation in flowering types when the inflorescences did not flower at the same time.

These harmonious successions of ♂ and ♀ phases within a tree did not occur if the tree also flowered on long shoots of the previous year (see par. 5).

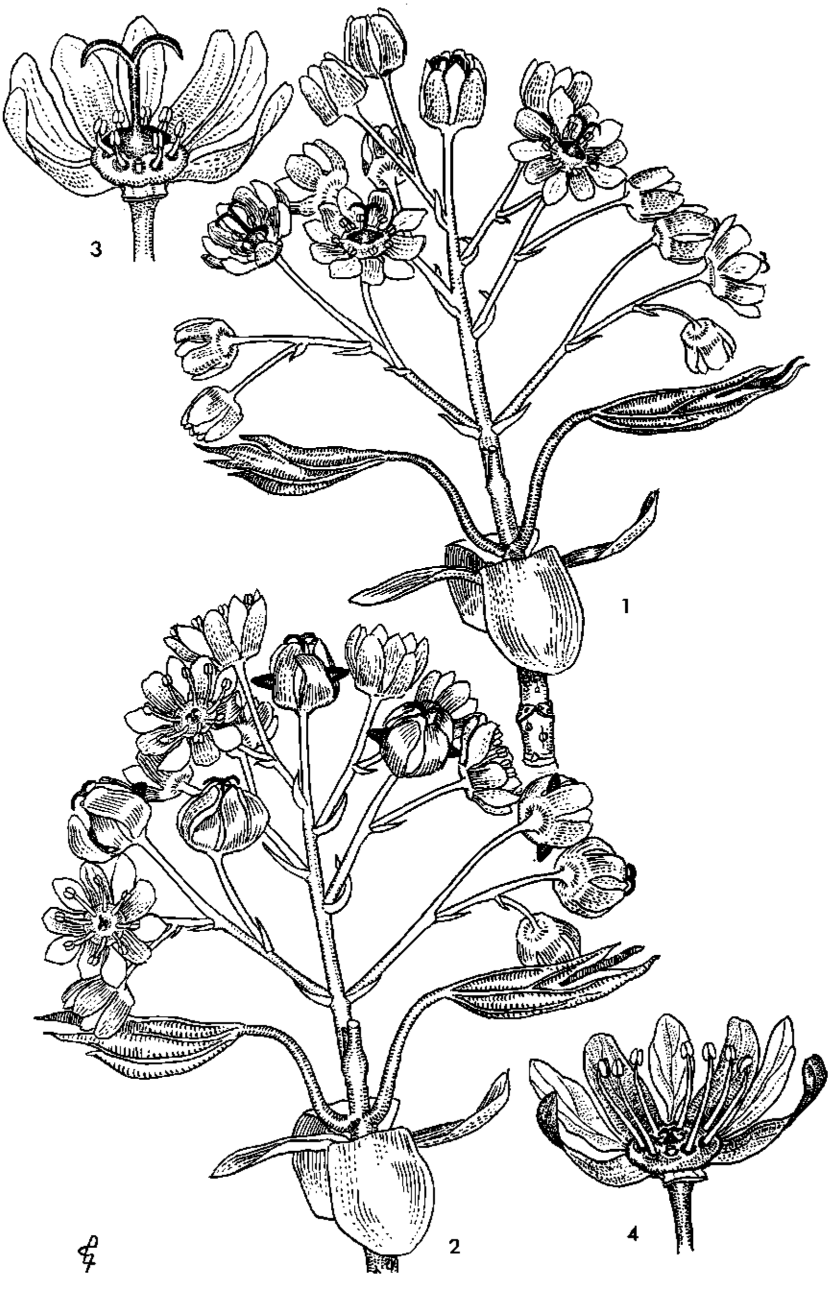


FIG. 12. *Acer platanoides* L.: Protogynous flowering specimen: 1–2. infl. ($1^1/_3\times$): 1. ♀ phase (April 28, 1969), 2. ♂$_{(\mathrm{II})}$ phase (May 2, 1969); 3–4. fl., one sepal and two petals removed (4×); 3. ♀ fl., 4. ♂$_{\mathrm{II}}$ fl. ('Schwedleri' Wag. B.G. no. 12041).

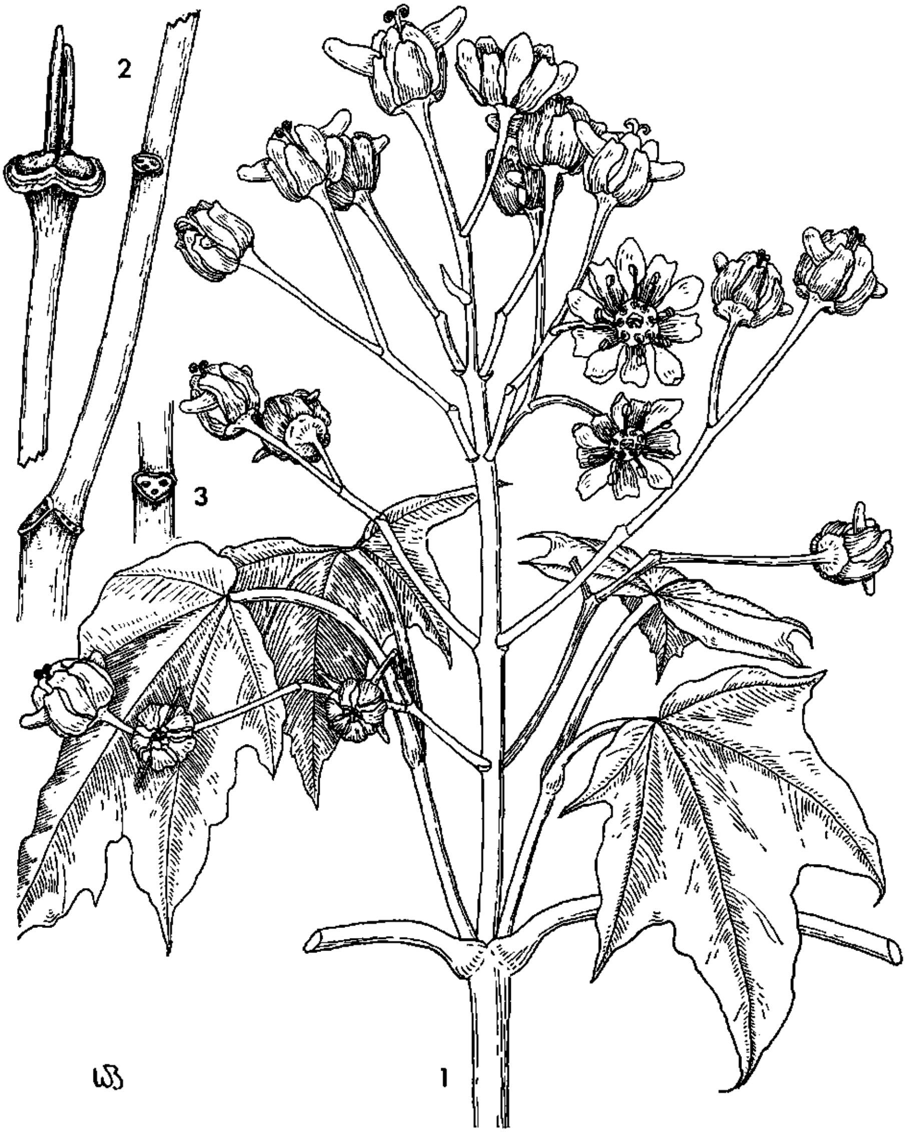


FIG. 13. *Acer platanoides* L.: Duodichogamous flowering specimen: 1. infl.: second ♂ phase ($1^1/_2\times$); 2. identification of duodichogamy (flowering type C) from old fruit stalks: near the basis scar of dropped terminal $♂_I$ fl. and ring-shaped scar of bract, near the top scar of dropped axillary $♂_{II}$ fl. ($7^1/_2\times$); 3. scar of $♂_I$ fl.: front view ($7^1/_2\times$). ('Reitenbachii' Wag. B.G. no. 12116).

It was never observed that isolated specimens of species of this series completely failed to fruit. It may be concluded from this observation that self-fertilization occurred and that some overlap of ♂ and ♀ phases must always be present within a single tree.

In figure 12 type B of 'Schwedleri' (no. 12041) is shown during both phases. The two types of 'Almira' (no. 14858) are represented in fig. 11. The inflorescence with type E has already finished flowering when the inflorescence of type D shows its ♀ phase. An inflorescence of type C, taken from 'Reitenbachii' (no. 12116), is shown during the second ♂ phase in fig. 13.

3. *Variations in flowering types*

Table 7 gives the results of 6 years of observations in the Wag. B.G. If more than one flowering type was found on a single tree, they are arranged in order of frequency. Trees rarely failed to flower in the observational period. The gaps in the table are due to young trees, which did not flower in the first few years, and to trees cut in later years. A lack of training as regards methodical observations during the first year (1966) caused incomplete results.

On the whole flowering was rather regular with only slight yearly variations. These variations were mainly caused by the length of the $♂_{I}$ phase and the number of flowers per inflorescence (see par. 4).

4. *Relation between flowering type, flowering time and number of flowers per inflorescence*

In paragraph 2 it was already mentioned that within a tree there was nearly no overlap of $♂_{I}$ and ♀ phases of flowers despite a varying flowering time of single inflorescences.

Counts were made on a young specimen of *A. plat.* 'Erectum' (no. 14862) in 1969 and 1970. In the first year all inflorescences were counted, on 2 May at the end of the $♂_{I}$ phase and on 8 May during the $♂_{II}$ phase. In 1970 only the inflorescences of some branches were counted, together about 1/3 of all inflorescences. This was done on 6 and 7 and on 11 May. The results are shown in table 8. In 1969 there were not only few inflorescences but they also had fewer flowers than in 1970 (25 against 33). Especially the large number of small inflorescences in 1969 caused the variations between these years. These inflorescences mostly ceased flowering some days before the ♀ phase. In 1970 a close relation between number of flowers per inflorescence and flowering type was absent. Inflorescences of type C started anthesis relatively late and had a small $♂_{I}$ phase. Because of the variable number of flowers per inflorescence nothing can be said about variations in the length of the $♂_{I}$ phase in these years.

In 1967 an interesting observation could be made of an extreme variation in start of flowering of inflorescences on a single tree at the 'Wageningse Berg'. When the tree had nearly ceased flowering two inflorescences were still in bud. These inflorescences represented type B while the other inflorescences were mainly type E and sometimes type D.

TABLE 7. Flowering types observed on specimens of series *Platanoidea* between 1966 and 1971 in the Wageningen Botanic Gardens.

species cultivar	garden number	flowering types (in order of frequency)					
		1966	1967	1968	1969	1970	1971
A. campestre							
'Elsrijk'	17863	B	B,F	B,F	B,F	B,F	B
'Elsrijk'	17863	B	B,F	B	B,F	B,F	B
'Nanum'	1766	E	E	E	E,D	E,D	E
'Zorgvlied'	17864	C	C,D,E	C,D	C,D	D,C	D,C
'Zorgvlied'	17864	C	C,D,E	+			
A. cappadocicum							
'Aureum'	8331	–	–	C	C,D	C,D	D,C
'Rubrum'	1776	C	C	C	C,D	D,C	+
A. lobelii	14665	C	C	C	D,C	D,E	D,C
A. miyabei	2754	D	D	D,C	D	C,D,F,G	D,C
A. mono	13275	B	B	B	B	B	B
A. platanoides							
'Almira'	14858	C	C,D	D,C	E,D	D,E,C	D,E,C
'Almira'	18080	C	C,D	D,C	+		
'Cleveland'	18078	–	E,D	E,D	–	E	G,E
'Crimson King'		–	–	–	B	B	B
'Erectum'	14862	C	E,D	D,C,E	E,D,C	D,E,C	D,E,C
'Faassen's Black'	13163	B	B	B	B,H	B	B
'Globosum'	11454	B	B	B	B	B	B
'Goldworth Purple'	8376	B	B	B	B	B	B
'Charles F. Irish'	18079	B	B	B	B	B	B
'Palmatifidum'	11457	B	C,B,D	+			
'Palmatifidum'	12076	B	C,B	B	B	B	B,C
'Reitenbachii'	1774	C	C,D	D,C	D,C	C,D	C,D
'Reitenbachii'	12216	C	C,D	D,C	D,C	C,D	C,D,B
'Schwedleri'	12041	B	B	B	B	B	B
'Schwedleri'	11455	B	B	+			
'Schwedleri'	12555	B	B	B	B	B	B
A. x zoeschense	11358	–	–	B	B	B	B
'Elongatum'	13277	–	–	–	B	B	B

– no flowers
\+ cut down

5. *Variations as a result of flowering on one-year-old long shoots*

Several trees occasionally flowered on vigorous shoots of the previous year. By contrast in some years some grafted and very fast growing young trees of *A. plat.* cv's were abundantly flowering on these shoots. The inflorescences appeared both terminally and laterally. Anthesis started 3–5 days later than on the other shoots, the lateral buds again starting somewhat later than the terminal inflorescences. The change to flowers of the other sex occurred on these vigorous shoots some days later than elsewhere in the tree.

In 1970 flowering of four trees was analysed. At some moment during flowering the progress of anthesis was determined by counts of flowers, blown

TABLE 8. Analysis of flowering of a specimen of *A. platanoides* 'Erectum' (Wag. B.G. no. 14862) in 1969 and 1970.

flowering type of inflorescences	number of inflorescences	mean number of flowers per inflorescences			
		♂I	♀	♂II	total
1969					
type C	1	20	10	6	36
type D	13	32	2		34
type E	88	24			24
ibid: out of flower on 2 May	13	18			18
ibid: with flower buds on 2 May	15	40			40
total number	102	25	0.3	0.1	25
1970					
type C	5	17	15	3	35
type D	86	34	4		37
type E	16	35			35
ibid: out of flower on 7 May	7	31			31
total number	107	33	4	0.2	37

TABLE 9. Analysis of flowering on normal shoots (N) and on long shoots of the previous year (L) of 4 specimens of *A. platanoides* in the Wageningen Botanic Gardens.

cultivar, garden number date of observations (category of shoots)	number of inflor.	mean number of flowers per inflorescence							
		blown ♂I	blown ♀	open ♀	in bud ♀	blown ♂II	open ♂II	in bud ♂II	total
'Faassen's Black (no. 13163) May 7, 1970 (N)	52		4			3	14	5	26
ibid. (L)	62		3	7				30	39
'Goldworth Purple' (no. 8376) May 7, 1970 (N)	30		7			7	9	5	27
ibid. (L)	12		13	0.5				30	43
'Schwedleri' (no. 12555) May 7, 1970 (N)	49		7			3	10	2	22
ibid. (L)	12		10	7	0.1		0.1	11	28
'Reitenbachii' (no. 12116) May 8, 1970 (N)	27	13	0.4	11				3	27
ibid. (L)	37	10		19	2			10	41
ibid. (L) from lateral buds	17	4		9	3			11	28
ibid. (L) from terminal buds	20	15		28	0.3			9	52

flowers and flowers buds of some long shoots and branches with normal young shoots on the same part of a tree. The results are shown in table 9.

The inflorescences of 'Faassens Black' (no. 13163), 'Goldworth Purple' (no. 8376) and 'Schwedleri' (no. 12255) were always of type B. The inflorescences on long shoots were still in the ♀ phase, while the inflorescences elsewhere in the tree were in the middle of the ♂ phase.

'Reitenbachii' (no. 12116) also showed variations in flowering types. The average number of ♂$_{I}$ flowers of lateral inflorescences was relatively low, some inflorescences had no ♂$_{I}$ flowers at all (type B). The number of flowers of the large terminal inflorescences on the vigorous shoots was twice the number elsewhere in the tree (52 against 27), while the number of ♂$_{I}$ flowers was nearly the same (15 against 13). The mean number of ♂$_{I}$ flowers on long and normal shoots showed a variation of 3 flowers per inflorescence. However, the length of the ♂$_{I}$ phase on long shoots was much shorter. The relatively high number of ♂$_{I}$ flowers on these long shoots was caused by the strongly deviating size of the terminal inflorescences. The flowering types on the long shoots were C and sometimes B, while the remaining part of the trees showed types C and D.

All specimens showed a higher mean number of flowers per inflorescence with comparatively much more ♀ flowers on the long shoots.

6. *Clonal varieties and rootstocks*

Clonal varieties of *A. plat.* and *A. campestre* showed a high degree of resemblance in their flowering. They had not only the same flowering types but also the start of anthesis and changes of ♂ and ♀ phases occurred simultaneously.

As no influence of seedling rootstock could be observed, the genetic constitution of the cultivar can be considered as the basis for its flowering and sex expression.

7. *Stability of protogynous flowering*

Trees which started flowering with ♀ flowers rarely showed variations. On only one tree ♂$_{I}$ flowers were found. *A. plat.* 'Palmatifidum' (no. 12076) had ♂$_{I}$ flowers in a limited number of the inflorescences in 1967 and one ♂$_{I}$ flower (!) in 1971. The ♂$_{I}$ flowers were restricted to the lower branches of the tree.

8. *Absence of a ♀ phase*

On specimens with a very short ♀ phase, ♀ flowers may be lacking in some small inflorescences with a relatively late anthesis: flowering type F. This condition is shown in fig. 14.1 for *A. campestre* 'Elsrijk' (no. 17863).

Occasionally inflorescences were found with ♂$_{I}$ and ♂$_{II}$ flowers (type G). In 1968 this phenomenon was observed on an *A. plat.* tree in 'Oranje Nassau Oord' at Wageningen. Inflorescences of type C on the lowest branches were mixed with those of type G. It was further observed that these lower branches were strongly shaded by shrubs.

In later years this type was only noticed again on two other trees. In 1971 *A. plat.* 'Cleveland' (no. 18078) had exclusively inflorescences with only ♂$_{I}$ and

FIG. 14. *Acer campestre* L.: Protogynous flowering specimen: 1–2. branchlets during ♂$_{(\mathrm{II})}$ phase ($1^1/_2\times$): 1. protogynous infl. (right) and ♂$_{(\mathrm{II})}$ infl. (left), 2. ♂ infl. with asexual terminal fl.; 3–6. fl. ($5\times$): 3. ♀ fl., 4. ♂$_{\mathrm{II}}$ fl.: early anthesis during ♂$_{\mathrm{II}}$ phase, large abortive pistil, 5. ♂$_{\mathrm{II}}$ fl.: late anthesis, small abortive pistil, 6. asexual fl. ('Elsrijk' Wag. B.G. no. 17863).

♂$_{II}$ flowers. This specimen, rather shaded by large oaks on the west side, produced ♀ flowers in previous years.

The other tree is *A. miyabei* (no. 2754). In 1970 this tree flowered abundantly. Some shoots also had small inflorescences from leafless lateral buds, which mostly had flowering types G and F. These inflorescences started anthesis relatively late. The other inflorescences of this tree had types D and C.

9. *Failure of sex expression on the borderline of the ♀ and ♂$_{II}$ phases*

This phenomenon was specially studied on *A. campestre* 'Elsrijk' (no. 17863). At the end of the ♀ phase the first buds to open, which already showed a small style, hardly developed further. There was also no lengthening of the pedicel. Such an asexual flower is shown in fig. 14, 2 and 6. In some trees of *A. plat.* occasionally the same observations, were made: 'Faassen's Black' (no. 13163) in 1970 and 'Reitenbachii' (no. 12116) in 1971.

Observations of these small asexual flowers are rather difficult because such flowers are very easily mistaken for buds. It may be possible that these flowers were also observed by WAHLENBERG (1820), who described hermaphrodite flowers with scarcily any (functional) sex expression (see footnote on pag. 17).

Sometimes after the first ♂$_{II}$ flowers had shed their pollen some of these backward flowers did extend one or more filaments and their anthers shed (fertil) pollen.

10. *An apparently ♂ flowering tree*

A. campestre 'Nanum' (no. 1766) was completely ♂ flowering during 7 of the 10 years of observations. In 1970 about 1 percent of the inflorescences had 1(–3) ♀ flowers (type D). In 1969 and 1971 such inflorescences occurred on only one branch, which was in a rather poor condition. The unfolding of the leaves and the start of anthesis were 3–5 days later than elsewhere in the tree. The ♀ flowers also appeared after all other inflorescences had finished flowering. After flowering this branch had a very poor appearance and several of its branchlets died during the summer. In 1972 the whole branch collapsed.

It was observed that the average number of flowers per inflorescence in 1970, the year with some ♀ flowers throughout the tree, was higher than in 1970 (14.4 against 11.4).

11. *Occurrence of a second ♀ phase*

In 1969 *A. plat.* 'Faassen's Black' (no. 13163) had some inflorescences with a second phase of ♀ flowers (type H). These ♀ flowers appeared all over the tree in inflorescences on normal shoots at the end of the flowering period.

12. *Degree of variability within the series*

Studies of sex expression of both living and herbarium specimens indicated that probably all species had the same variability in their flowering. Male flowering specimens were rarely observed.

The observed protogynous specimens showed a high degree of stability but it may be possible that this picture will change after an extensive study, as made on *A. pseudoplatanus*.

B. Series Pubescentia

The species of this series were exclusively studied from herbarium specimens (see specimens examined).

The inflorescences developed from mixed terminal and lateral buds. The proportion of the latter was considerable. They were often very small and emerged partly from leafless buds. The flowers had petals which were curved inwards. The disc is lobed and the 5 stamens were inserted between the lobes. Of 26 specimens studied 13 flowered protogynously (type B). The remaining 13 specimens had started anthesis with ♂ flowers. Some of these had many unopened buds, others represented flowering types C and D.

III. Section Palmata

1. *Introduction and literature*

This section, greatly extended by OGATA (1967), contains a large number of species with some very characteristic morphological features. Because a large number of species are limited to subtropical areas, most species had to be studied from herbarium material only.

The living specimens studied were mainly cultivars of *A. palmatum*, especially those at the 'Sortimentstuin' of the Nursery Experiment Station at Boskoop. Some other specimens belonged to the species *A. circinatum*, *A. japonicum* and *A. oliverianum*. The ratio of trees with a ♂ and a ♀ start of flowering were determined on herbarium specimens of *A. circinatum*, collected at natural stands. The same was done for a number of South-East Himalayan specimens (see par. 7).

A determination of the flowering types on fruiting (herbarium) specimens was rather difficult when the cincinni had only one fruit each. When such single fruits had two scars on their stalks these scars could originate both from two preceding ♂$_{I}$ flowers (type D) and from one preceeding ♂$_{I}$ flower and one (or several) succeeding ♂$_{II}$ flowers (type C).

The species of this section were usually described as monoecious. HAAS (1933) observed 12 specimens of *A. circinatum* which showed the flowering types C and a single one with type B. Despite the isolated locations of these specimens seedy fruits were produced. WRIGHT (1953) noticed that the dichogamous pattern found in *A. platanoides* was also typical of *A. japonicum* and *A. palmatum*.

2. *General observations on flowering*

A. japonicum was the earliest flowering species of this section in The Netherlands. Anthesis started about mid April and partially coincided with that of *A. platanoides*. The remaining species started flowering some days later.

Strictly morphologically the species of this section usually have no terminal buds. After a premature abortion of this bud the shoots have two or one well-

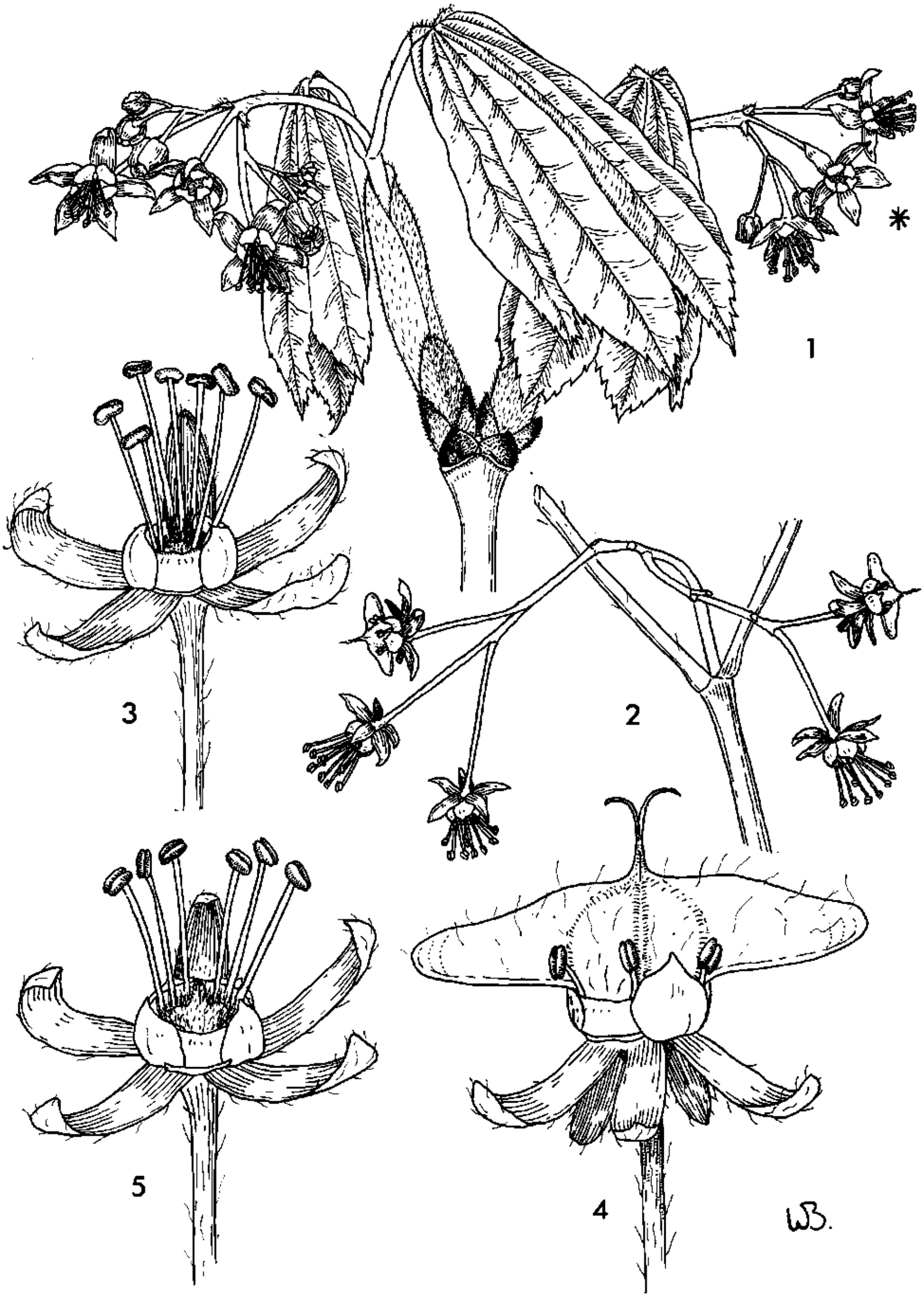


FIG. 15. *Acer circinatum* Pursh.: Duodichogamous flowering specimen: 1. infl. during ♂$_{\mathrm{I}}$ phase;* blown fl. with dropped stamens (May 5, 1969) ($1^1/_2$ ×); 2. infl. during ♂$_{\mathrm{II}}$ phase (May, 14, 1969) ($1^1/_2$); 3–5. fl., one petal removed (6×): 3: ♂$_{\mathrm{I}}$ fl., 4. ♀ fl., 5. ♂$_{\mathrm{II}}$ fl. (Wag. B.G. no. 17525).

developed lateral buds at the tip. Consequently all inflorescences emerge from lateral buds. Because these lateral buds replace the aborted terminal bud they can better be considered as terminal buds.

The inflorescences emerged from these mixed terminal buds and on long shoots of the previous year partly from lateral buds. Anthesis started simultaneously with the unfolding of the leaves or some days later.

The cymous structure of the inflorescences (see 2.3.1 and fig. 16) led to a rather long flowering period, because the flowers of the cincinni opened very gradually. The observations on blown ♂ flowers are described in 2.3.3.

It was found that isolated monocious specimens of several species produced fruits, which indicated the occurrence of self fertilization.

3. *Variations in flowering types*

Table 10 shows the result of 6 years of observations. Some young plants failed to flower during the first few years of observations.

Within single trees overlap of ♂ and ♀ phases was mainly caused by flowering on long shoots of the previous year. On *A. japonicum* (no. 12681) the observations were rather similar to those described for *A. plat.* 'Reichenbachii' (see II Plat., par. 6). On normal shoots the inflorescences represented types D, C and E, while those on long shoots represented C and B.

4. *Clonal varieties on rootstocks*

Of some cultivars (*A. palm.* 'Osakazuki' and *A. jap.* 'Aconitifolium') several specimens could also be studied elsewhere, e.g. at the Zuiderpark. They were found to show the same degree of resemblance in their flowering as earlier mentioned for cv.'s of *A. platanoides* and *A. pseudoplatanus*. There was also no influence on the sex expression of the seedling rootstocks.

5. *Stability of protogynous flowering*

Although some trees were protogynous in all years of observation some others were so variable that they could neither be considered as protogynous nor as trees with an ♂ start of flowering, e.g. *A. palm* 'Dissectum' (no. 12679), 'Nicholsonii' and 'Osakazuki'. The length of the $♂_1$ phase was highly variable.

From these observations on a rather low number of specimens it is impossible to draw conclusions about the degree of instability within this section.

6. *Two male A. palmatum cv.'s*

The two studied specimens of the clonal varieties 'Decompositum' and ('Palmatum') flowered ♂ during all years of observation. Physiological experiments indicated that these specimens were genetically male (see 5.2.3).

7. *Variability in A. circinatum.*

A. circinatum often has very uniform inflorescences, which produce one or two fruits. The inflorescences have a short rachis with two cincinni with 3–5 flowers each (see 2.3.1 and fig. 15).

TABLE 10. Flowering types observed on specimens of section *Palmata* between 1966 and 1971 in the Boskoop Nursery Experiment Station and the Wageningen Botanic Gardens.

species cultivar	garden number (Wag. B.G.)	flowering types (in order of frequency)					
		1966	1967	1968	1969	1970	1971
A. circinatum	15725	C	C,D,E	C,D	C,D	C,D	C,D,E
A. japonicum	12681	D	E,D	C	C,B	C,D,B	C,D
'Aconitifolium'		—	C,D,B	C	C	C,D,E	C
'Veitchii'		—	C,B	—	C	C,B	C
('Vitifolium')		—	—	C	C,B	C,D,E	—
A. palmatum							
'Atropurpureum'	12253	—	C	C	C,B	C	C
'Atropurpureum'		C	C	C	—	C	C
'Bloodgood'		—	—	—	C	C	—
'Decompositum'		—	—	E	E	E	E
'Dissectum'	12254	—	C,B	B	B	B	B,C
'Dissectum'		—	—	B	B	B	B
'Dissectum nigrum'		—	—	—	C	B,C	—
'Dissectum paucum'		—	B	B	B	B	B
'Dissectum rubrifolium'		—	B	B	B	—	B
'Dissectum rubrum'		C	B	C	C	B	C
'Dissectum variegatum'		B	B	—	B	B	B
'Elegans'		B	B	B	B	B,F	B
'Elegans'		B	B	B	B	B	B
'Elegans purpureum'	12679	—	—	B	B	B	B
'Elegans purpureum'		—	B	B	B	B	B
'Laciniatum purpureum'		B	B	B	B	B	B
'Linearilobum'		C	C	C	B	C,D	C
'Nicholsonii'		B	C,B	B	B	B	B
'Osakazuki'	14711	B	C,B	—	B,C	C,B	B
'Osakazuki'		B	B,C	B	B	C,B	C,B
'Osakazuki'		B	B,C	B	B	B,C	C,B
('Palmatum')		—	—	E	E	E	E
'Reticulatum'	14702	—	—	—	C	C	C
'Reticulatum'		—	—	B	B	C	—
'Roseomarginatum'		—	B	B	B	B	—
'Rufescens'		C	E,D	B	B	C	C
'Sanguineum'		—	—	—	—	C	C

— no flowers

In case of protogynous flowering the single ♀ flower is the terminal flower of the rachis. A fruiting specimen shows solitary fruits above the leaves. The short straight stalks have two scars of the dropped cincinni.

When flowering starts with a ♂ phase, the small ♀ phase consists of one flower, mostly the third, fourth of fifth flower of each cincinnus. The samaras of such specimens have long tortuous stalks with 3–5 scars respectively.

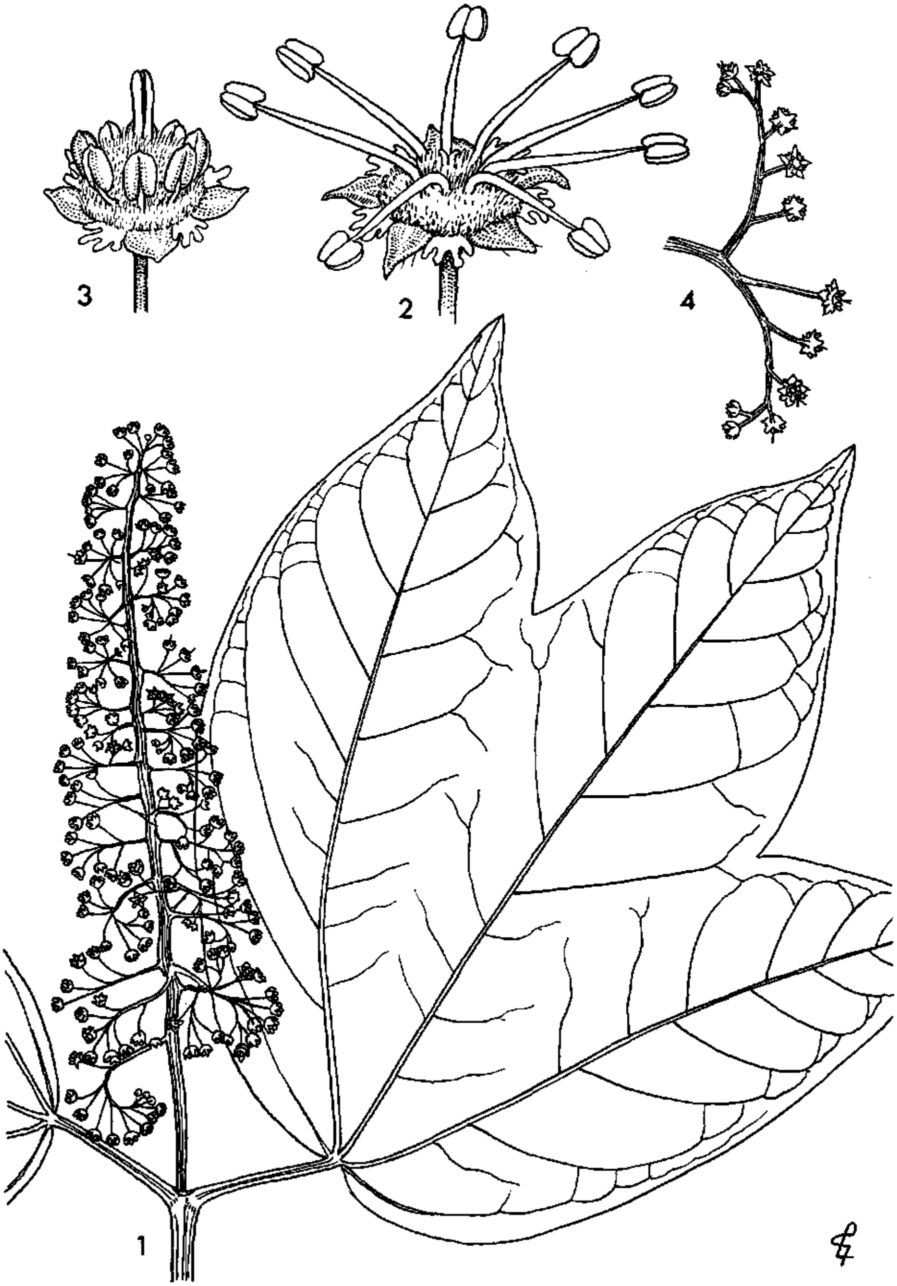


FIG. 16. *Acer tonkinense* Lecomte: 1. branchlet ($^5/_6\times$); 2. ♂$_I$ fl.: disc hairy, petals lobed, white, sepals and anthers red ($10\times$); 3. ♀ fl. bud a few days before anthesis ($10\times$); 4. part of infl.: scorpioid ramification ($2^1/_2\times$). (Stewart & Cheo 152, BM).

Larger inflorescences, which will mainly be found on long shoots of the previous year, have more than two cincinni and, consequently, more fruits.

A number of 45 herbarium specimens, collected at natural stands in North America, were examined for flowering type. There were 20 specimens with a ♂ and 19 specimens with a ♀ start of anthesis, while 6 specimens showed both possibilities. Six specimens had only ♂ flowers.

8. *Degree of variability within the section*

The variability as found in *A. circinatum* and *A. palmatum* does not hold for the whole section, e.g. the series *Penninervia* and *Sinensia*. Some species of the Southeastern Himalayas have very large inflorescences with 150–300 flowers, especially *A. sinense* and *A. tonkinense* (see fig. 16), and also *A. campbellii*, *A. erianthum*, *A. flabellatum* and *A. laevigatum*. All specimens studied were monoecious, predominantly with a ♂ start of anthesis.

IV. **Section Macrantha**

A. **Series Tegmentosa**

1. *Introduction and literature*

The flowering of the various species of this series was rather difficult to analyse. Of all species the number of specimens was limited, but the studied species showed a large degree of resemblance in their flowering and morphology. Besides observations on flowering specimens of collections in Belgium and The Netherlands, the sex expression was also studied after flowering during visits to French and English Botanic Gardens and Arboreta. The sex expression of inflorescences of herbarium specimens was examined in collections from natural habitats of the species of this series (see par. 5).

The information on the sex expression in this series is scarce and contradictory. SARGENT (1891, 1905) reporting about the flowering of *A. pensylvanicum* stated that the ♂ and ♀ flowers were usually produced on different racemes on the same plant. Both WITTROCK (1886) and HAAS (1933) also studied one single specimen of this species. The former observed that some small ♂ inflorescences appeared one and a half weeks after the tree flowered completely ♀. The latter observed the ♂ and ♀ flowers simultaneously. The ♂ flowers had relatively large abortive pistils.

Most taxonomists obtained their knowledge of flowering in this series from the few herbarium specimens available. KOIDZUMI (1911) described the Japanese species as dioecious except *A. tschonoskii*. REHDER (1905) regarded *A. davidii* as apparently monoecious, *A. maximowiczii* as apparently dioecious and the remaining species as dioecous. FANG (1939), too, described most Chinese species as dioecious. *A. davidii*. *A. kawakamii*, *A. rufinerve*, *A. tegmentosum* and *A. tschonoskii* were monoecious. OGATA (1965, 1967) considered the series as mainly dioecious. Monoecy was occasionally observed by him in single specimens of the Japanese species *A. crataegifolium*, *A. morifolium* and *A. tschonoskii*.

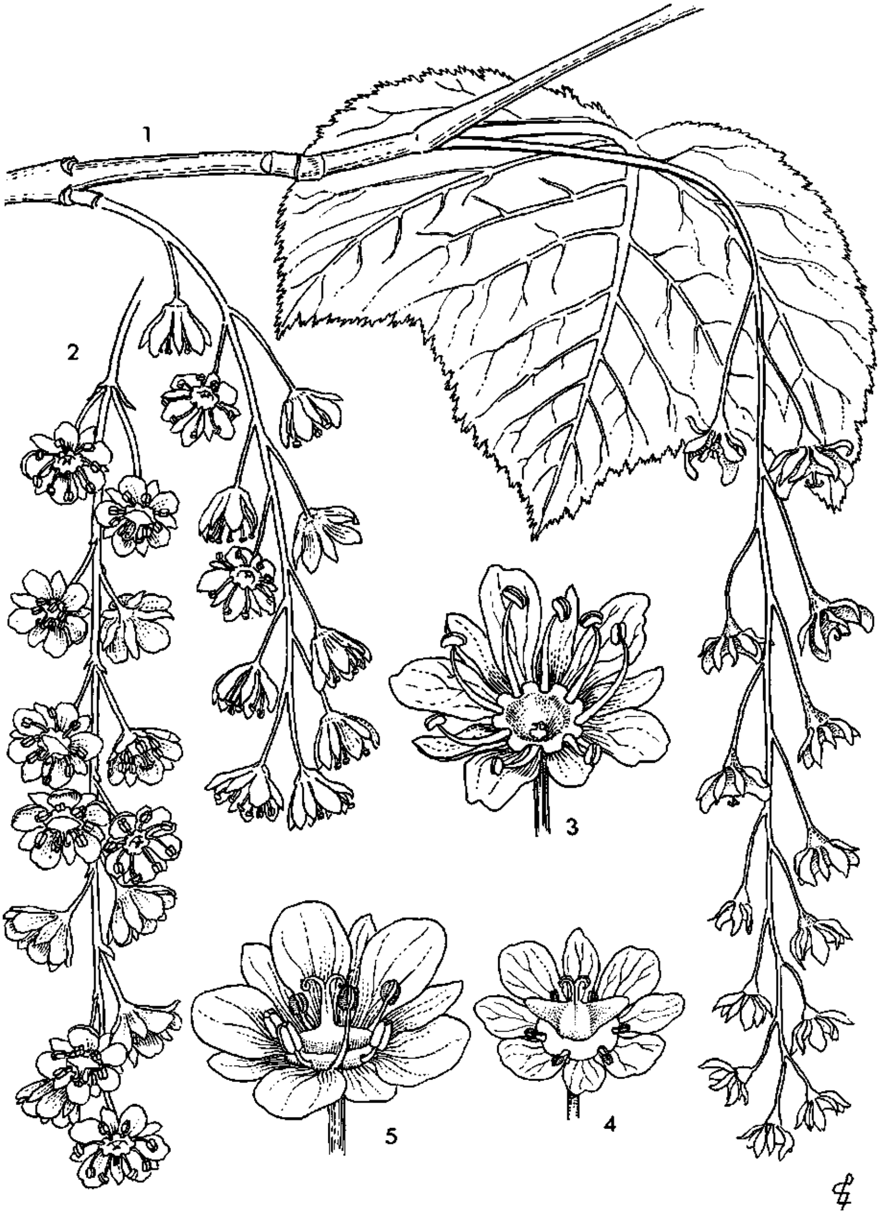


FIG. 17. *Acer pensylvanicum* L.: 1. branchlet with ♀ infl. developed from mixed terminal bud and ♂ infl. from leafless axillary bud ($1^1/_3\times$); 2. polygamous infl. (♂, ♀ and ☿ fl.) ($1^1/_3\times$); 3–5. fl. (4×): 3. ♂, 4. ♀, 5. ☿. (Zuiderpark: 1, 3, 4 no. II; 2, 5 no IV).

2. *General observations on flowering*

The inflorescences appeared from terminal and lateral buds and were accompanied by one pair of leaves. The lateral inflorescences sometimes emerged from leafless buds, especially in *A. pensylvanicum* (see fig. 17). Depending on the precocity of flowering the flowers opened simultaneously with the unfolding of the leaves (e.g. *A. rufinerve*) or up to 6 weeks later (e.g. *A. micranthum*). The flowering period of the whole series lasted from the end of April to mid June.

The racemose structure of the inflorescences (see 2.3.1) led to a short period, in which all the flower buds opened. On short racemes flowering started with the terminal bud. By contrast the terminal flower of long racemes opened rather late during anthesis. The nearly simultaneous flowering of the flowers of individual inflorescences usually led to unisexual inflorescences.

At first sight monoecious flowering specimens could have the ♂ and ♀ inflorescences on separate branches with an overlapping or simultaneous anthesis. An analysis could only start after the finding of androgynous inflorescences. These inflorescences were sometimes found in transitional zones from ♂ to ♀ flowering parts of trees. They flowered proterandrously, but often with some overlapping of ♂ and ♀ phases. Although toe ♂ flowers preceded the ♀ ones and therefore must be considered as ♂$_{\mathrm{I}}$ flowers, these flowers had rather large abortive pistils such as are found in the ♂$_{\mathrm{II}}$ flowers of the previous sections (see fig. 17, 18, 19 and 21). Because androgynous inflorescences were always protandrous, ♂ inflorescences could only have ♂$_{\mathrm{I}}$ flowers. A second ♂ phase did not occur in this series.

Detailed observations on monoecious flowering specimens showed that on the same branch a zone with ♂ inflorescences in the upper parts sometimes passed into a transitional zone with androgynous inflorescences with an increasing number of ♀ flowers per inflorescence until finally the inflorescences were completely ♀. This is shown in fig. 19 for *A. forrestii* (no. 14360). Dichogamy was more complete in androgynous inflorescences than between ♂ and ♀ flowering parts of the trees. Flowering of these parts started rather simultaneously.

A transitional zone with androgynous inflorescences was usually absent in *A. pensylvanicum* (see fig. 17). Besides ♂ and ♀ flowering parts specimens of this species showed branches with different ratios of ♂ and ♀ inflorescences. It was observed that the ♂ inflorescences of such branches partly emerged from leafless lateral buds (see fig. 17,1).

Predominantly ♂ flowering specimens produced their ♀ flowers mainly on some slender branches in the lower parts of the tree. In predominantly ♀ flowering trees the ♂ flowers appeared on one or two branches in the upper part of their crown.

The large yearly variations in sex expression and the variation within a single tree are described in paragraphs 3 and 4 respectively.

3. *Annual variability in the sex expression*

Several specimens were observed for 2–6 years. The results are shown in

FIG. 18. *Acer grosseri* Pax: 1. branchlet with ♂ infl. and fruit stalks of the previous year (2×); 2. androgynous infl. with part of the ♂ fl. dropped (2×); 3. ♂ fl. (5×); 4. ♀ fl. (5×). (Wag. B.G. no. 13067-I).

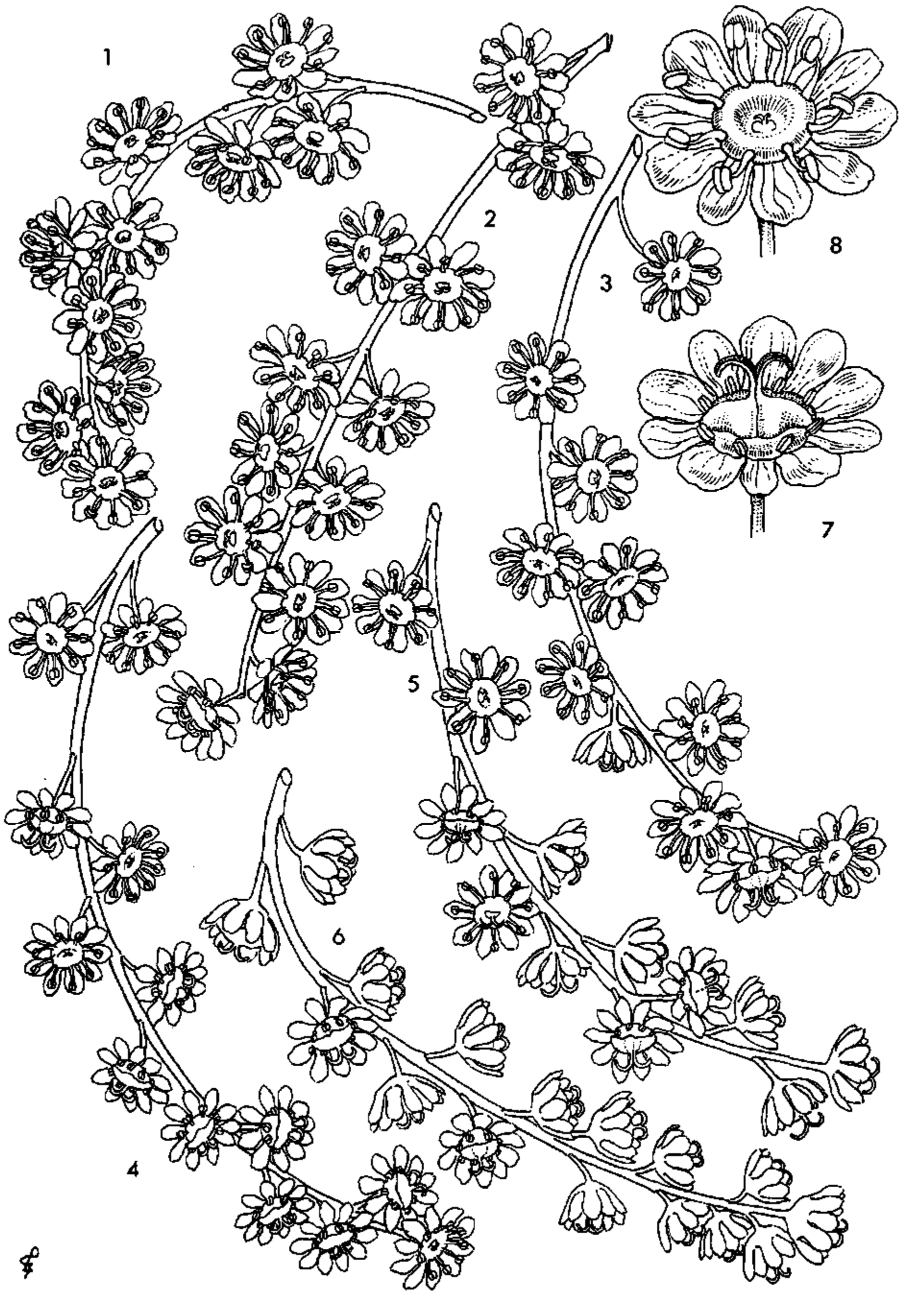


FIG. 19. *Acer forrestii* Diels: 1–6. infl. (2×): 1. ♂ infl., 2.5. androgynous infl.: decreasing ♂/♀ ratio, 6. ♀ infl.; 7. ♀ fl. (5×); 8. ♂ fl. (5×). (Wag. B.G. no. 14360).

Table 11. Flowering types observed on specimens of series *Tegmentosa* at the Wag. B.G. (W), the Gimborn Arb. (G), the Zuiderpark (Z) and the Kalmthout Arb. (K).

species	(garden), garden number or association number	flowering types (in order of frequency)					
		1966	1967	1968	1970	1970	1971
A. capillipes	(W) no. 13270	A,E	A	A	A	A	A[1]
A. capillipes	(W) no. 17783						A,D[2] [4]
A. forrestii	(W) no. 14360	A	A,E,D	A	A,E,D	A	A
A. grosseri (hybr.)	(W) no. 12997	A	A,E	A	A		A[1]
A. grosseri	(W) no. 13067-I	E	E,A,D	E,A	E	E,D,A	E,A,D
A. grosseri	(W) no. 13067-II	A	A	A	A	A	A[1] [4]
A. grosseri	(W) no. 14782	A	A,E	A	A	A	A[1]
A. grosseri	(W) no. 17788				A	E,A	E,A,D
A. grosseri (hybr.)	(W) no. 15500	A	A,E,D	A	A	A	A,E,D,[1]
A. grosseri (hybr.)	(K) no. 822					E,A,D	
A. grosseri (hybr.)	(K) no. 811					E[5]	
A. maximowiczii	(G) s.n.					E	
A. micranthum	(W) no. 17530			E	E,A,D	E,A,D	E,D
A. micranthum	(G) I				E,A,D	A,D	A
A. micranthum	(G) II				E,A,D	D,A,E	A,D
A. pensylvanicum	(W) no. 12283	A	A	A	A	A	A
A. pensylvanicum	(W) s.n.				E,A	A	A[1]
A. pensylvanicum	(Z) I				E[5]	A,E	E,A
A. pensylvanicum	(Z) II				E,A	A	E,A
A. pensylvanicum	(Z) III				A,E	A	A
A. pensylvanicum	(Z) IV				A,E	A,E	A,E
A. pensylvanicum	(Z) V					A,E,D	A
A. pensylvanicum	(Z) VI					A	A
A. rufinerve	(W) no. 11357	A	A	A	A	A	A,E
A. rufinerve	(W) no. 12471	A	A,E,D	A	A	A	E,A[2]
A. rufinerve	(Z) 'Albolimbatum'				A,E	A	A[1]
A. rufinerve	(Z) I				A,E	A,E,D	A,E[1]
A. rufinerve	(Z) II				A,E	A	A[2]
A. rufinerve	(Z) III				A	A	A[1]
A. tschonoski	(K) s.n.				D	A	

[1] 1974 A
[2] 1974 A,E
[3] 1972–3 A, D, E; 1974 E
[4] 1973 A,E,D
[5] fruit stalks of the previous year

table 11. Most specimens flowered monoeciously in at least one year of the observational period. *A. pensylvanicum* no. 12283, ♀ flowering in all years of observation, flowered monoeciously in previous years and seedlings were grown from it (personal communication Mr. W. J. M. Jansen, formaly curator of Wag. B.G.). *A grosseri* no. 17168-I flowered completely ♀ between 1966 and 1975, except in 1973.

The yearly variations showed some shift in a certain direction. In 1969 flowering was predominantly ♀ and in 1970 (and 1974) a large proportion of ♂ flowers were observed. However, flowering of all specimens did not show the same tendency. In 1970 the three studied specimens of *A. micranthum* flowered monoeciously with about the same proportions of ♂ and ♀ flowers. In 1971 the Wageningen specimen mainly had ♂ flowers, while the Gimborn specimens were predominantly ♀. In some successive years of monoecious flowering the distribution of ♂ and ♀ inflorescences did not change. This resulted in the occurrence of some heavily fruiting branches with old fruit stalks of previous years and of other branches without fruits and without old fruit stalks. This continuous division showed no relation with various ecological conditions. For example it was frequently observed that a shrub with two or more main branches produced its ♂ or ♀ flowers on one branch only. The ramifications of this branch could be such that ♂ and ♀ flowering branches were scattered over several parts of the crown.

Such patterns could also be observed on a large number of fruiting specimens during visits to Botanic Gardens and Arboreta in Belgium, England and France for *A. capillipes*, *A. davidii*, *A. forrestii*, *A. grosseri*, *A. pensylvanicum* and *A. rufinerve*. Fig. 18,1 shows a ♂ inflorescence on a branchlet with an old fruit stalk of the previous year.

It was observed that in case of monoecious flowering self-fertilisation always occurred. Isolated fruiting specimens of *A. crataegifolium*, *A. hookeri*, *A. maximowiczii*, *A. rubescens*, *A. tschonoskii* were observed. In contrast with the occurrence of self-fertilization is the great ability for interspecific hybridizations within this series.

4. *The variation in sex expression within a single specimen.*

The juvenile phase of seedlings of the species studied is rather short. Seedlings of various species already flowered when they were 3–5 years old. During the period in which young trees show a rapid development part of the inflorescences will be produced on lateral buds of vigorous shoots. The terminal inflorescence of such shoots started anthesis before the lateral inflorescences. The uppermost lateral inflorescences in their turn flowered earlier than lower inflorescences on the same shoot. In fig. 21 and 22 shoots are shown of different parts of the tree, on which anthesis started simultaneously with ♂ and ♀ flowers. The ♂ flowers were succeeded by a ♀ phase: see fig. 22. The terminal inflorescence, on which anthesis of the shoot started, had only few ♀ flowers, including one produced by ramification of one of the lowest pair of secondary axes (see fig. 22, 4). The uppermost pair of lateral inflorescences had predominantly ♀ flowers. The remaining lateral inflorescence, developed from a leafless bud, was still in bud at that time. This inflorescence only had ♀ buds.

The variation in stage of development of the inflorescences of the monoecious flowering shoots also led to variations in the sex expression of their inflorescences. These observations agree with those in the previous sections, e.g. *A. plat.* 'Reitenbachii' on which the terminal inflorescences of long shoots of the previous year had a longer ♂$_{I}$ phase than the lateral ones.

By contrast, it appears unlikely that the development of the inflorescences on complete ♀ flowering shoots lagged behind so strongly that as a result ♂$_{I}$ flowers

FIG. 20. *Acer micranthum* S. & Z.: Protandrous flowering branchlet ($1^{1}/_{2}$): 1. ♂ infl., nearly simultaneous anthesis of all fl.; 2. androgynous infl., the basic part of the rachis with the ♀ fl. (buds) lagging behind in development. (Wag. B.G. no. 17530).

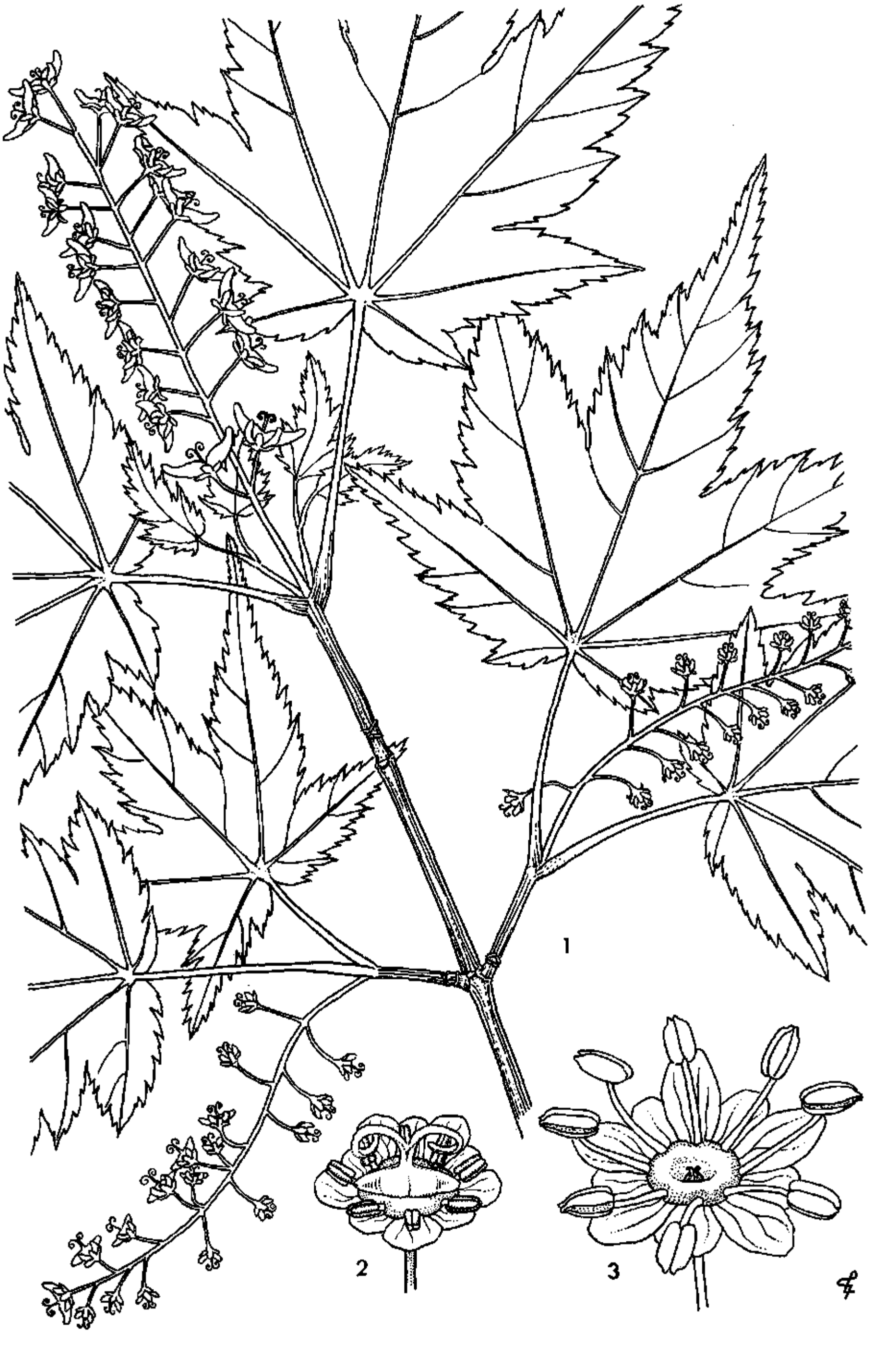


FIG. 21. *Acer micranthum* S &. Z.: 1. branchlet with ♀ infl. (June 15, 1970) ($1^1/_3$×); 2. ♀ fl. (8×); 3. ♂ fl. (8×). (Gimborn Arb. no. II).

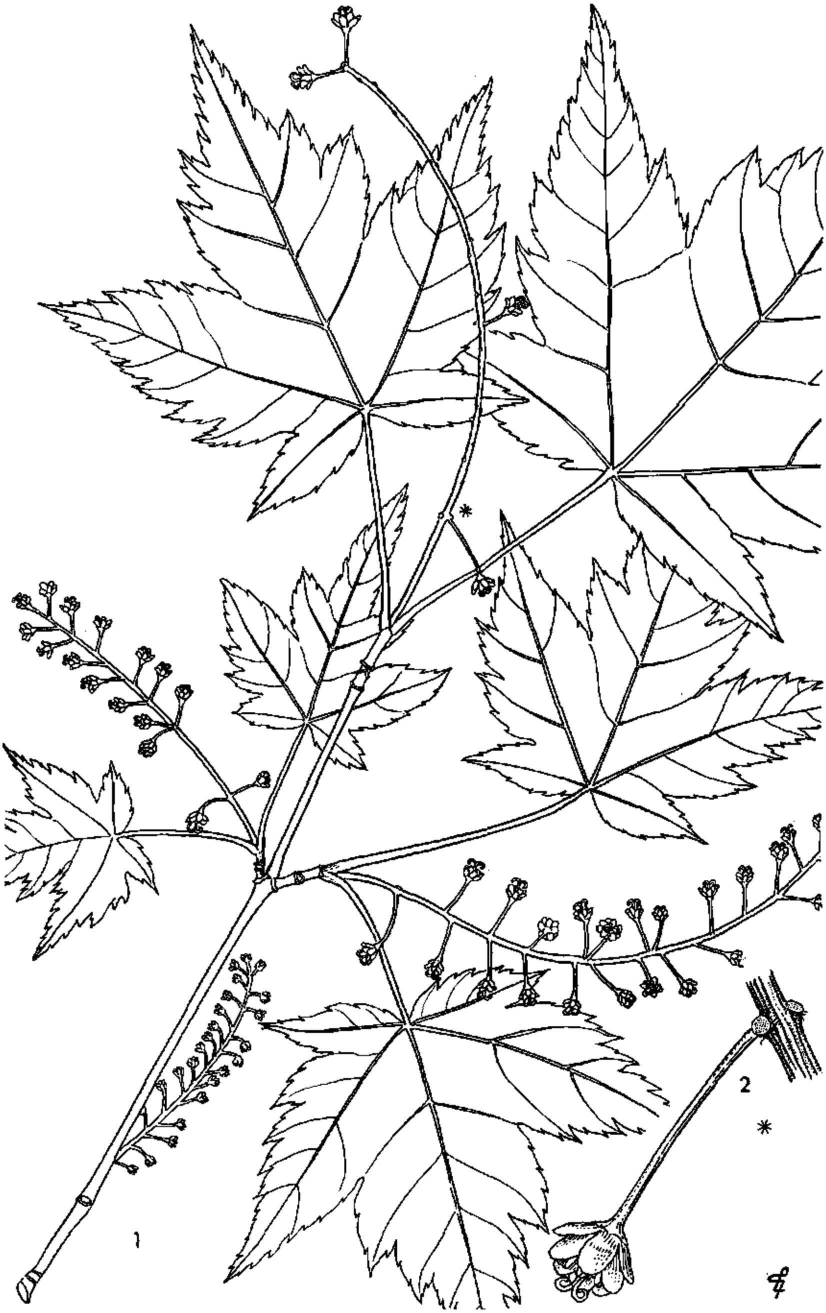


FIG. 22. *Acer micranthum* S. & Z.: 1. branchlet with protandrous terminal infl. (blown ♂ fl. dropped) and ♀ axillary infl. (June 15, 1970) ($1^{1}/_{3}$); 2. tertiary axis (♀ fl.), scar of dropped secondary axis (♂$_{\mathrm{I}}$ fl.) (5 ×). (Gimborn Arb. no. II).

would be absent. This question will be discussed again after studies on sex differentiation (see 5.7).

5. *Occurrence of bisexual flowers*

Functional ☿ flowers were found in one Zuiderpark specimen of *A. pensylvanicum* in 1970. They were observed in inflorescences which also produced ♂ and ♀ flowers (see fig. 17, 2 and 5). In addition androgynous inflorescences were only rarely found in this species. Pollen was not germinated.

6. *Degree of monoecious flowering within the series*

In all species of which living specimens were available, monoecious flowering was observed. After 8 years of observations at Wageningen it could be said that all specimens had produced flowers of both sexes in at least one of these years or before this observational period. The observations at Kew Gardens in 1970 and several Arboreta in the S.W. of the United Kingdom in 1973 showed that at least half the number of specimens had flowered monoeciously in these years. On the basis of the results of table 11 it can be stated that, if each observation was treated as an individual observation, monoecy was found in 35 percent of all observations.

In contrast with this high frequency of monoecy, observed in West European gardens, the percentage of monoecious flowering specimens in natural habitats tends to be rather low. The sex expression of more than 250 herbarium specimens was studied and only 11 specimens flowered monoeciously. Among them four sheets had androgynous inflorescences: *A. davidii*: Yunnan, G. Forrest 10045 and 22599 (K); Szechuan, W. C. Cheng 942 (K); Kiangsi (K), Stewart 2620. One specimen of *A. rufinerve* had ♂ and ♀ inflorescences: Hondo, S. Togasi 1007 (K) and six specimens had ♂ inflorescences and old fruits stalks: *A. crataegifolium*: Hiyagosa, Bisset 1036 (BM) and Senano, Tschonoski s.n., (BM;) *A. davidii*: Szechuan, Farges 140 (P) and Hupeh, Henry 5336 (BM); *A. micranthum*: Kyoto, Hotta 14871 (P) and *A. sikkimense*: Yunnan, Forrest 26233 (K).

The considerable variation in degree of monoecious flowering between these herbarium specimens from the natural areas and the results of observations in West-European Gardens indicate a possible influence of the ecological conditions. But what will be the effect when material is collected by people who are not familiar with this phenomenon?

SARGENT (1891, 1905) described *A. pensylvanicum* as usually monoecious, but all studied herbarium specimens had only ♂ or ♀ inflorescences. Collectors such as Farges, Maximowicz, Tschonoski and Wilson combined shoots with ♂ and ♀ inflorescences (and fruits) of different specimens under the same field number.

Studying several living specimens OGATA (1965, 1967) found very few monoecious individuals.

The very close taxonomic relations of the species in this series makes it likely that all species may have the ability to flower monoeciously. Androgynous inflorescences are always proterandrous, so protogyny does not occur in this series.

B. Series Wardiana

The single species of this series. *A. wardii*, could only be studied from herbarium sheets. The inflorescences were developed from mixed terminal and lateral buds. The secondary axes had small cincinni and were strictly opposite. The limited number of herbarium specimens, which were available, had flowers of one sex only, but the rather primitive inflorescence may be an indication of a possible occurrence of monoecy in this series.

V. Section Parviflora

A. Series Parviflora

The single species of this series. *A. nipponicum*, is very rarely cultivated. One specimen could be studied in the Zuiderpark at The Hague.

The sex expression of *A. nipponicum* was described by Koidzumi (1911) as 'andropolygamous' indicating a condition with ♂ and monoecious flowering specimens. Ogata (1965) observed a number of trees of this species at Mt. Kurohime, Nagano Pref., Japan, in 1961. All the trees had ♂ inflorescences and no ♀ flower was found.

From 1969–1973 the present author observed the flowering of the Zuiderpark specimen, a tree of about thirty years old. The very large drooping inflorescences with 150–300 flowers appeared from mixed terminal buds and sometimes from mixed lateral buds. During the first 2–3 weeks of anthesis all inflorescences bore exclusively ♂ flowers (see fig. 23.1). A number of the inflorescences produced ♀ flowers at the end of the flowering period (see fig. 23.2). The ♂ and protrandrous inflorescences (types E and D respectively) were mostly produced on separate branches. The latter inflorescences mostly had a distinct division between the ♂ and ♀ phases, but some large ♂ inflorescences could still flower during the ♀ phase of the protrandrous inflorescences. In 1970, 1972 and 1973 the few ♀ flowers appeared very late, while ♂ flowers were not longer present for pollination.

All fourteen herbarium specimens studied had inflorescences with a very long $♂_{\mathrm{I}}$ phase or were completely ♂. Despite the large number of flowers – Ogata (1965) noted up to 400 or more, rarely up to almost 1000 – a second ♂ phase was nearly absent. A few $♂_{\mathrm{II}}$ flowers were observed on two specimens: Sidesan, Faurie 2311 (P, W) and Hondo, Wilson (K, BM). It was also observed that during the ♀ phase of an inflorescence some cincinni continued to produce $♂_{\mathrm{I}}$ flowers.

The absence of a protogynous sex expression and the rare occurrence of $♂_{\mathrm{II}}$ flowers supply arguments for a relationship of this species with the series *Tegmentosa.*

B. Series Ukurunduensia

Of this series only one flowering specimen of *A. spicatum* could be studied at Wag. B.G.

In literature the species of this series were considered as monoecious. Koidzumi (1911) used the term 'andropolygamous' indicating the occurrence of

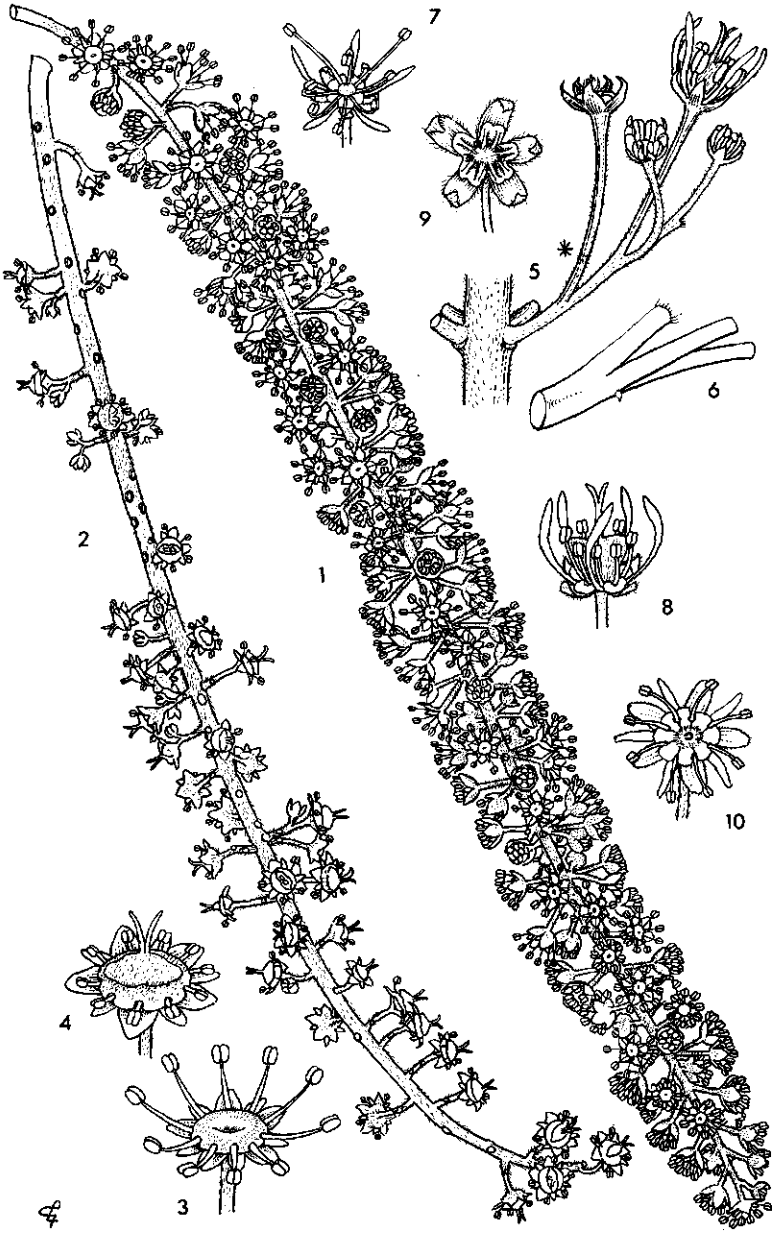


FIG. 23. *Acer nipponicum* Hara: 1.2. protandrous flowering infl. (1$^{1}/_{3}$) 1.: ♂$_{\rm I}$ phase (June 10, 1970), 2. ♀ phase (June 26, 1970); 3. ♂$_{\rm I}$ fl. (4×); 4. ♀ fl. (4×). (1-4-Zuiderpark).
Acer spicatum Lam.: 5. cincinnus during ♀ phase, blown ♂$_{\rm I}$ fl.: see 8. (4×); 6. cincinnus after abscission of ♂$_{\rm I}$ fl. (8×); 7. ♂$_{\rm I}$ fl. (4×); 8. ♀ fl. (4×); 9. ♂$_{\rm I}$ fl. (blown): petals and stamens dropped, disc showing insertion of 3 stamens in the middle of episepalous lobes (8×). (5–9. Wag. B.G. no. 12290).
Acer distylum S. & Z.: 10. ♂$_{\rm II}$ fl., amphistaminal disc with stamens inserted between the lobes (4×). (Wilson 70002, K).

♂ and monoecious flowering specimens. OGATA (1965) reported that the specimens of *A. ukurunduense* observed in the mountains of Chicubu in Saitama Pref., at Mt. Kurohime in Nagano Pref. and elsewhere in Japan, flowered ♂ or monoeciously. Apparently he could find no difference between the growing sites of both types of specimens.

The studied *A. spicatum* (no. 12290) flowered between the end of May and mid June about four weeks after the unfolding of the leaves. The erect inflorescences appeared from mixed terminal buds and partly from mixed lateral buds. The structure of these large inflorescences with 100–250 flowers resembled that of some *Palmata* species, e.g. *A. erianthum* and *A. sinense* (see fig. 16). Blown ♂ flowers dropped stamens and petals first (see fig. 23,5 and 9). After several days the rest of the flower with a part of the pedicel dropped (see fig. 23, 6 and 2.3.3).

The inflorescences mainly represented type C, while in some years a few inflorescences of type B were found. The latter started anthesis during the ♀ phase of the remaining inflorescences.

Studies of herbarium specimens collected at natural habitats showed domination of protandrous flowering specimens. Of 82 *A. spicatum* specimens 72 were protrandrous and 10 protogynous. The Asiatic species yielded in all 30 protandrous and 3 protogynous specimens. The protandrous specimens also include some completely ♂ flowering specimens, while the flowering types of some of these specimens could not be established because a number of the inflorescences partly had unopened flowers. Despite the observed ♂ flowering specimens (genetic) ♂ specimens probably rarely occur in this series. Male flowering may be mainly caused by environmental conditions.

Series Distyla

The single species of this series, *A. distylum*, could only be studied from herbarium specimens.

In literature the species is described as monoecious.

The inflorescences have a long rachis with several small cincinni, as observed for *A. nipponicum* and *A. spicatum*, but the number of flowers (25–75) is lower than in the latter species.

Of 14 specimens studied, 9 had protogynous inflorescences (type B). Two specimens were protandrous (types D and D or C respectively). The remaining 3 specimens just started anthesis with $♂_I$ flowers.

VI. Section Trifoliata

1. *Introduction and literature*

Rather few living specimens were present in Dutch Gardens while also herbarium material was scarce. Yet interesting observations on *A. griseum* and *A. maximowiczianum* (syn. *A. nikoense*) were possible. The strong tendency to parthenocarpy (see 2.5.2) enabled a study of the sex expression of isolated fruiting specimens after the flowering period.

The notes on sex expression of the species of this section are few and contradictory. MAXIMOWICZ (1867, 1880), REHDER (1927), FANG (1939) and OGATA (1965, 1967) considered the section as dioecious. PAX (1885) described the section as monoecious, although he also placed the dioecious *A. cissifolium* in it. KOIDZUMI (1911) regarded the section as monoecious or dioecious, but described *A. maximowiczianum*, the only studied species, as dioecious. Finally TURRILL (1962), who prepared the accompanying text for a plate of *A. maximowiczianum* in Curtis Botanical Magazine, described these species as 'andromonoecious', i.e. monoecious. He further reported that the material for the plate was collected in the Royal Botanic Gardens at Kew. The present author found the original material in the Kew Herbarium. The ♂ and ♀ inflorescences were collected from a garden specimen with association number 000-69-10324. It is very likely that TURRILL only based the monoecious flowering of this species on observations in the Kew Gardens.

2. *General observations on flowering*

The flowering of *A. griseum* and *A. maximowiczianum* started some days before or simultaneously with the unfolding of leaves between the middle and the end of May. The individual branches of a single tree sometimes showed a variation in the start of anthesis of about a week. The small inflorescences with mostly 3 flowers emerged from mixed and leafless buds. Both species usually had accessory buds at the tip of vigorous shoots. On such shoots inflorescences also developed from lateral buds, which were sometimes leafless.

Despite the fairly close relation between these two species their flowering showed one interesting point of difference. On specimens of *A. maximowiczianum* a phase of ♀ flowers was never followed by $♂_{II}$ flowers. Androgynous inflorescences always had flowering type D, i.e. a ♂ terminal flower and two ♀ flowers. Monoecious flowering specimens of this species mostly had branches with predominantly or exclusively ♂ or ♀ flowers. The '♂' and '♀' branches sometimes flowered simultaneously, by contrast, branches carrying both sexes only showed overlap of '♂' and '♀' phases.

The androgynous inflorescences of *A. griseum* represented types D and B. Within the trees this species also showed some variation between the branches; types B and D were not found on the same branches. The inflorescences with type F appeared at the end of anthesis on poorly developed branches. The various flowering types of this species are shown in fig. 24.

3. *Annual variation in flowering*

During the period 1969–1971 specimens were studied at the Wag. B.G., the Gimborn Arb., the Zuiderpark and a public garden near the Ruigrocklaan in The Hague. In 1970 a *A. griseum* specimen was studied at the Kalmthout Arboretum. The results of the observations are shown in table 12.

Mr. S. G. A. Doorenbos,who planted all the (seedling) specimens in The Hague, observed the sex expression of these specimens for several years. He found monoecious flowering in *A. griseum* but never in *A. maximowiczianum*.

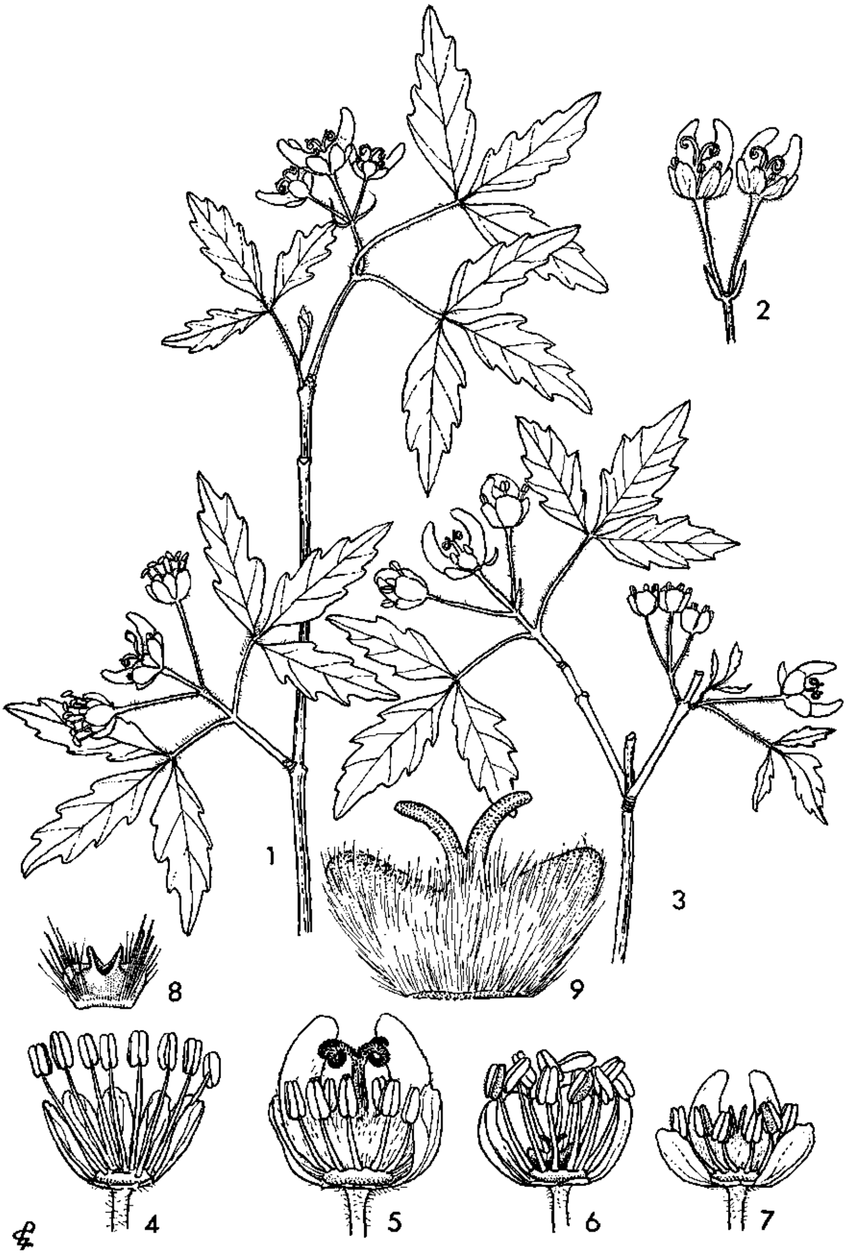


FIG. 24. *Acer griseum* (Franchet) Pax: 1. branchlet with a ♀ and a protogynous infl. ($^{5}/_{6}\times$); 2. protandrous infl., blown terminal (♂) fl. dropped ($^{5}/_{6}\times$); 3. branchlet with in the centre an infl. with ♂$_{II}$ fl. just before anthesis, at left protogynous infl. with abnormal ♂$_{II}$ fl. (see 7) ($^{5}/_{6}\times$); 4–7. fl., perianth partly removed ($2^{1}/_{2}\times$): 4 ♂$_{I}$ fl., 5. ♀ fl., 6. ♂$_{II}$ fl., 7. ♂$_{II}$ fl., strong pistil development; 8–9. pistils ($15\times$): 8. ♂$_{I}$ fl.: ovary scarcely hairy, 9. ♂$_{II}$ fl.: ovary densely hairy. (1, 2, 4, 6–9. Zuiderpark no. I; 3, 5. Wag. B.G. no. 14324).

TABLE 12. Flowering types observed on specimens of section *Trifoliata*

garden, garden number or association number	flowering types (in order of frequency)			
	1969	1970	1971	Other years
A. griseum				
Wag. Bot. Gard. no. 14324	A	A,B,F	A,B	
Wag. Bot. Gard. no. 15496	–	D	–	
Zuiderpark, I	A,B	A,B,F,(D?)	A,B,F	
Zuiderpark, II	A,B	A,B,F	A,B,D,F	
Ruigrocklaan		A,B,(D?)	A,B	
Kalmthout Arboretum no. 825		A,B,F		
A. maximowiczianum				
Wag. Bot. Gard. no. 794	E,D,A	E,D,A	E	1966-8; 1972-5:E
Wag. Bot. Gard. no. 14031	–	E,A,D	A	
Gimborn Arboretum	E,D,A	E,D,A	E,D,A	
Zuiderpark, I	E	E	E,A	1974: E
Zuiderpark, II	E,A,D	A,E,D	E,A	1974: E,D,A
Zuiderpark, III	E	E	E	1974: E,D,A
Zuiderpark, IV	E	E	E	1974: E
Zuiderpark, V	E	E	–	1974: E
Ruigrocklaan, I		E,D	E,A,D	
Ruigrocklaan, II		–[1])	E,A,D	

[1] fruit stalks of the previous year

The Zuiderpark specimens I, III-V and Ruigrocklaan I of the latter species were regarded as ♂ and the remaining specimens as ♀. The about 60-year-old specimen at Wageningen (no. 794) was only known as ♂ and fruits had never been observed before 1969. In that year the tree had one poor branch inside the crown with 3 ♀ inflorescences. In 1970 some more ♀ flowers were observed on the lowest branches of the tree and again on the branch with ♀ flowers in 1969. In all following years the tree flowered completely ♂, while the poor branch with ♀ flowers in 1969 and 1970 died. In 1971 the two specimens near the Ruigrocklaan, had the same flowering types at about the same ratios, while they had been known before as ♂ and ♀ individuals. In 1974 no. I flowered ♂ and no. II predominantly ♂. The Zuiderpark specimens flowered ♂ in 1974, except nos. II and III which were monoecious with predominantly ♂ flowers. The monoecious flowering of *A. griseum* was mainly caused by the occurrence of ♂$_{II}$ flowers. Most of the specimens studied were protogynous. In 1971 the Zuiderpark specimen no. II had a small ♂$_{I}$ phase on some branches.

The annual variations may be attributable to the environment but the small number of observations does not give further indications about the factors involved.

4. *Degree of variability within the section*

In contrast with the observed monoecy on living specimens the studied herbarium material collected at the natural stands was never monoecious. The only exception was a specimen of *A. sutchuenense* (Wilson 639, K) which had ♂ inflorescences and some small inflorescences with ♀ buds.

In the visited West European Gardens *A. griseum* and *A. maximoxiczianum* were predominantly monoecious. Seedy fruits were collected from several isolated specimens, including the specimen at Kew, of which the flowers were used for Curtis Bot. Mag. (see par. 1). The studied specimens of *A. maximowiczianum* mostly had their fruits on particular branches, while other branches only showed the scars of dropped (♂) inflorescences. The few studied specimens, of *A. mandshuricum* and *A. triflorum* had seedless fruits. It was mentioned in a personal communication with Mr. H. HILLIER that the single specimen of *A. triflorum*, on a very isolated spot in the Jermyn Arboretum, had produced in some years a few fruits from which seedlings were grown.

The degree of monoecious flowering in the natural areas seems to be much lower than in the West European Gardens.

The flowering of *A. maximowiczianum* showed the same pattern as found in the unrelated series *Tegmentosa*.

VII. Section Rubra

1. *Introduction and literature*

Although the two studied species, *A. rubrum* and *A. saccharinum* showed mutual variation in some aspects of their flowering they will be treated together. Of the former only a small number of living specimens could be studied. The observations on monoecious trees of the latter species were hindered by the distribution of the ♂ flowers in the upper parts of the crowns. The use of a 7 × 50 prisma viewer was indispensable.

The literature on the sex expression in this section seems rather contradictory. The first notes were given by MEEHAN (1879a), who described *A. rubrum* as dioecious. He studied the sex expression of 110 young trees, of which 69 were ♂ and 41 ♀. In the case of *A. saccharinum* MEEHAN found, besides ♂ and ♀ flowering trees, also monoecious specimens. The ♂ trees never had ♀ flowers, while ♀ flowering trees sometimes had ♂ flowering branches. The anthers of ♀ flowers of both species never shed pollen.

SARGENT (1892) noticed that both species had the ♂ and ♀ flowers in separate clusters, sometimes together and sometimes on different trees. In a special note on *A. rubrum* he mentioned further: 'The flowers of the Red Maple are usually described as polygamous and it is possible that perfect flowers occasionally occur on this tree.'

HEIN (1907) studied some thirty trees scattered about Lincoln, Nebraska (USA). The ♂ and ♀ flowers occurred in separate clusters but always on the same tree, the former being much more numerous. All trees produced their ♂ flower several days earlier than the ♀ flowers. The ♂ flowers were found from 28 March to 15 April, and the ♀ flowers from 5 April to 18 April. Hein examined 1000 ♂ and 200 ♀ flowers under a dissecting microscope. The number of stamens in ♂ flowers varied from 4–7. A rudimentary pistil was commonly found in ♂

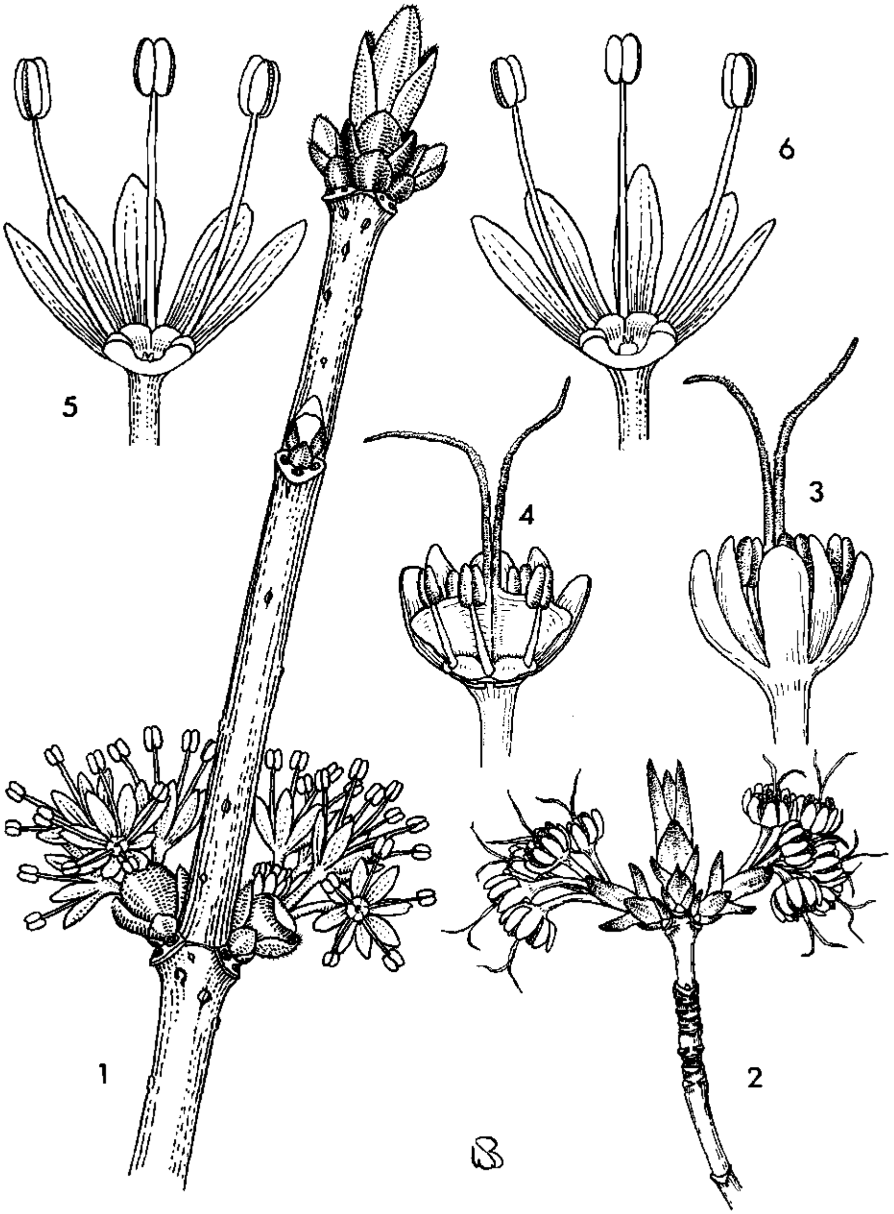


FIG. 25. *Acer rubrum* L.: Dioecious specimens: 1. branchlet, ♂ infl. (3×); 2. branchlet, ♀ infl. (2×); 3–6. fl. (6×): 3. ♀ fl., 4. ♀ fl., perianth partly removed, 5–6. ♂ fl., longitudinal section. (2–4. 'Sanguineum' Wag. B.G. no. 7809; 1, 5. 'Schlesingeri' Wag. B.G. no. 11472; 6. Wag. B.G. no. 7811).

flowers with 4 stamens. He remarked in this connection: 'This pistil is usually dwarfed and quite commonly mishapen, but sometimes it is perfect and matures into a well-formed, two-seeded fruit'. It may be supposed that the latter observation concerned ♀ flowers, because HEIN did not distinguish androgynous inflorescences. The ♂ flowers with five stamens mainly had rudimentary pistils consisting of a small knob covered with long white hairs, while occasionally only the hairs were found. The six-stamined ♂ flowers showed little trace of any rudimentary pistil and ♂ flowers with 7 stamens lacked any trace of it. Of the five ♂ flowers of a fascicle the central one, if any, generally bore the pistil whenever a rudimentary pistil was found, the stamens were mostly reduced or backward in their development. The observed trees had on average 7–10 per cent ♂ flowers with rudimentary pistils. In one tree they lacked completely. The ♀ flowers had 1–4 stamens, which were sometimes very small Most stamens of a ♀ flower were non-functional, but often one, and sometimes two stamens produced pollen. The anthers of such flowers were always retarded in their development. They did not shed pollen until the pistil had grown to a considerable size and probably had been pollinated from neighbouring ♂ flowers (see further par. 5).

HAAS (1933) observed at Munich 100 trees of *A. saccharinum*, which all flowered monoeciously with various ratios of ♂ and ♀ flowers, mostly on separate branches. He sometimes observed androgynous inflorescences and also such functional ♂ flowers with large abortive pistils as described by the present author for *A. pseudoplatanus* (see fig. 10). He further observed three young trees of *A. rubrum*, which flowered ♂ and three old trees with ♀ flowers only. The flowers of the latter trees shed pollen, but set no fruit. He also found one monoecious specimen of *A. rubrum*, which showed its ♀ flowers some days before the ♂ flowers.

WRIGHT (1953) reported that the trees of both species mainly flowered ♂ or ♀, although some had both types of flowers. He observed a tendency toward dioeciousness rather than toward dichogamy.

KOBENDZA (1953) found ♂, ♀ and monoecious flowering trees of *A. saccharinum* at Warsow, Poland. The monoecious specimens sometimes produced the ♂ and ♀ flowers on separate branches, while usually the ♀ flowers prevailed. He also observed that ♀ flowers had no stamens, or, if they were present, they had short filaments and scattered their pollen 'at a time other than' that of the ripening of the stigma.

MUSHEGIAN (1953) analysed the flowering of monoecious *A. saccharinum* specimens at Alma Ata. He distinguished four types of flowers: 1. ♂ flowers with 6 stamens; 2. functional ♂ flowers with a rudimentary pistil; 3. ♀ flowers and 4. male sterile flowers. The functional ♂ and ♀ flowers were mainly found in androgynous inflorescences, in any case androgynous inflorescences never lacked such flowers. It should be further noticed that both descriptions and figures showed inflorescences with four instead of five flowers.

HUTNIK and YAWNEY (1961) reported that the ♂ and ♀ flowers of monoecious *A. rubrum* specimens tended to be localized on different branches. The (♀)

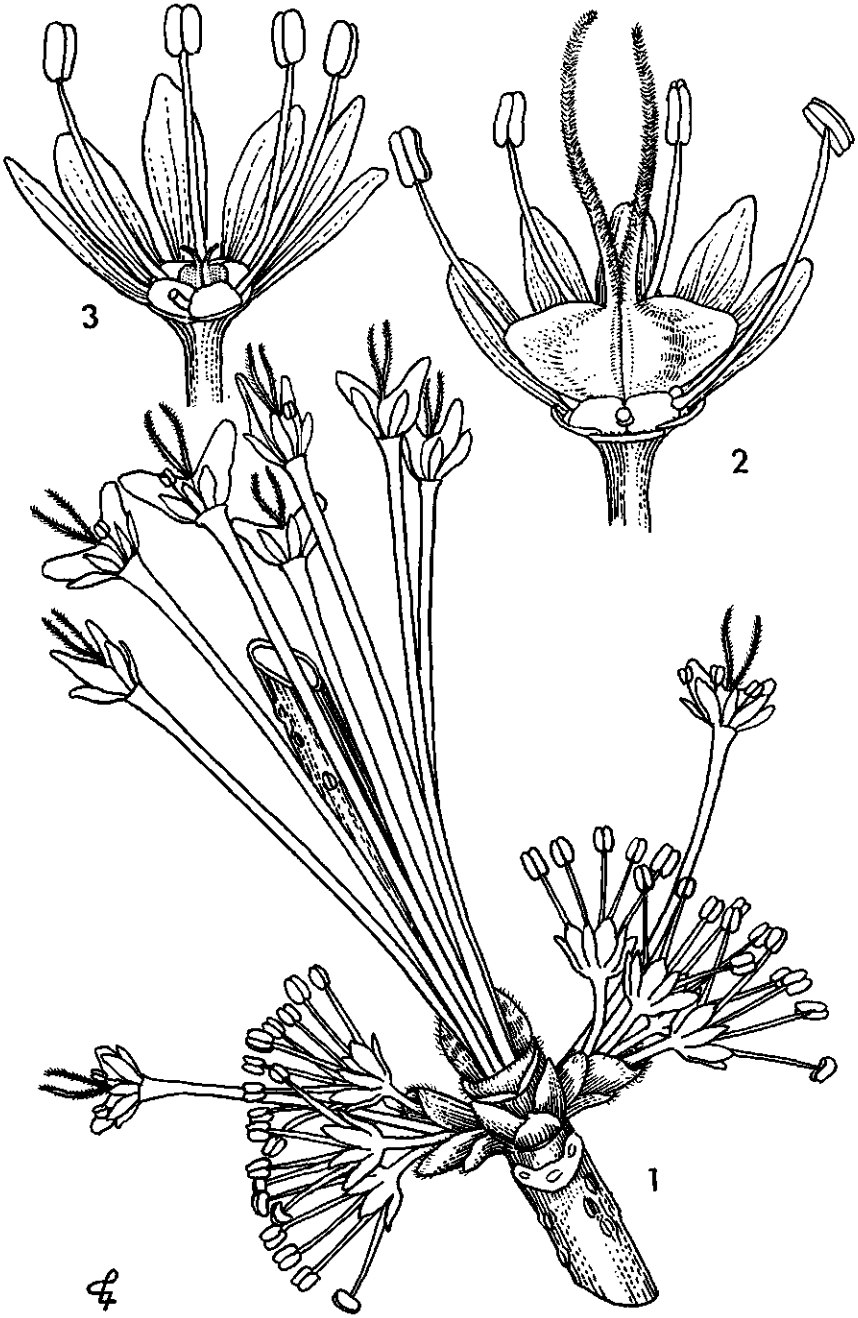


Fig. 26. *Acer rubrum* L.: Polygamous specimen: 1. branchlet with 3. infl. developed from one axillary bud, protogyny (forced into flower indoors) (3×); 2. ☿ fl. (9×); 3. ♂$_{II}$ fl. (9×). (Wag. B.G. no. 1757).

flowers were never functionally bisexual. HALL (1967) reported that most of the trees of both the species, *A. rubrum* and *A. saccharinum*, were predominantly dioecious. All the flowers of a single tree became functional within a day or two without showing a sexual rhythm as in e.g. *A. platanoides*. Several taxonomists considered the section as dioecious (e.g. PAX, 1885, 1902; KOIDZUMI, 1911; SCHNEIDER, 1905; OGATA, 1967). BOOM (1965) described *A. rubrum* as dioecious and *A. saccharinum* as monoecious.

2. *General observations on flowering*

A. saccharinum was the earliest flowering maple in the Netherlands. Depending on the weather conditions the flowers appeared between mid February and the end of March. *A. rubrum* started flowering from some to several days later, partly overlapping the flowering of *A. saccharinum* in some years. The inflorescences appeared from leafless lateral buds. The original lateral buds often branched further forming a cluster of inflorescences.

The single inflorescences were umbels (see 3.1.1) with mostly 5 flowers. The flowers of *A. rubrum* were stalked and had red sepals and petals. *A. saccharinum* had nearly sessile flowers. The whitish sepals were mostly completely connate. Petals were usually wanting, but 1–3 narrow petals were sometimes observed (see fig. 27). The ♂ flowers had long white filaments, strongly contrasting with the greenish-red or bright red stigmas of ♀ flowers. This difference was very useful to distinguish ♂ and ♀ flowers when watching the trees with a prisma viewer. The flower stalk of ♀ flowers of both species elongated after flowering in case of fruitset.

It was observed that if the temperature rose above 15°C the flowers of *A. rubrum*, which have a small disc, were frequently visited by bumble bees and honey bees.

In case of monoecious flowering the ♂ flowers mainly appeared in the upper part of the crown. If these ♂ flowers were numerous they could also be found on lower branches. The lowest, hanging branches of *A. saccharinum* trees only produced ♀ flowers.

Of *A. rubrum* only two trees of one clone flowered monoeciously. It was found that androgynous inflorescences represented type B. All ♂ flowers had rather large rudimentary pistils. In fig. 26 three inflorescences from one lateral bud are shown. The terminal one is completely ♀, the lateral ones are androgynous with at left a ♀ flower in the centre of the umbel. The corresponding branch was forced into flower indoors. This led to a clearer picture of protogynous flowering than could be observed on the tree itself. Protogynous flowering mainly occurred in androgynous inflorescences and on predominantly ♀ flowering branches. Flowering started simultaneously with ♂ and ♀ flowers on separate branches, moreover on predominantly ♀ flowering branches ♂ flowers also appeared some days later at the tip of these branches.

These observations on *A. rubrum* also hold for *A. saccharinum*. Fig. 27,1 shows a branchlet with ♂, ♀ and androgynous inflorescences. The ♂ flowers of the androgynous inflorescence with 3 ♂ and 2 ♀ flowers (shown in the centre)

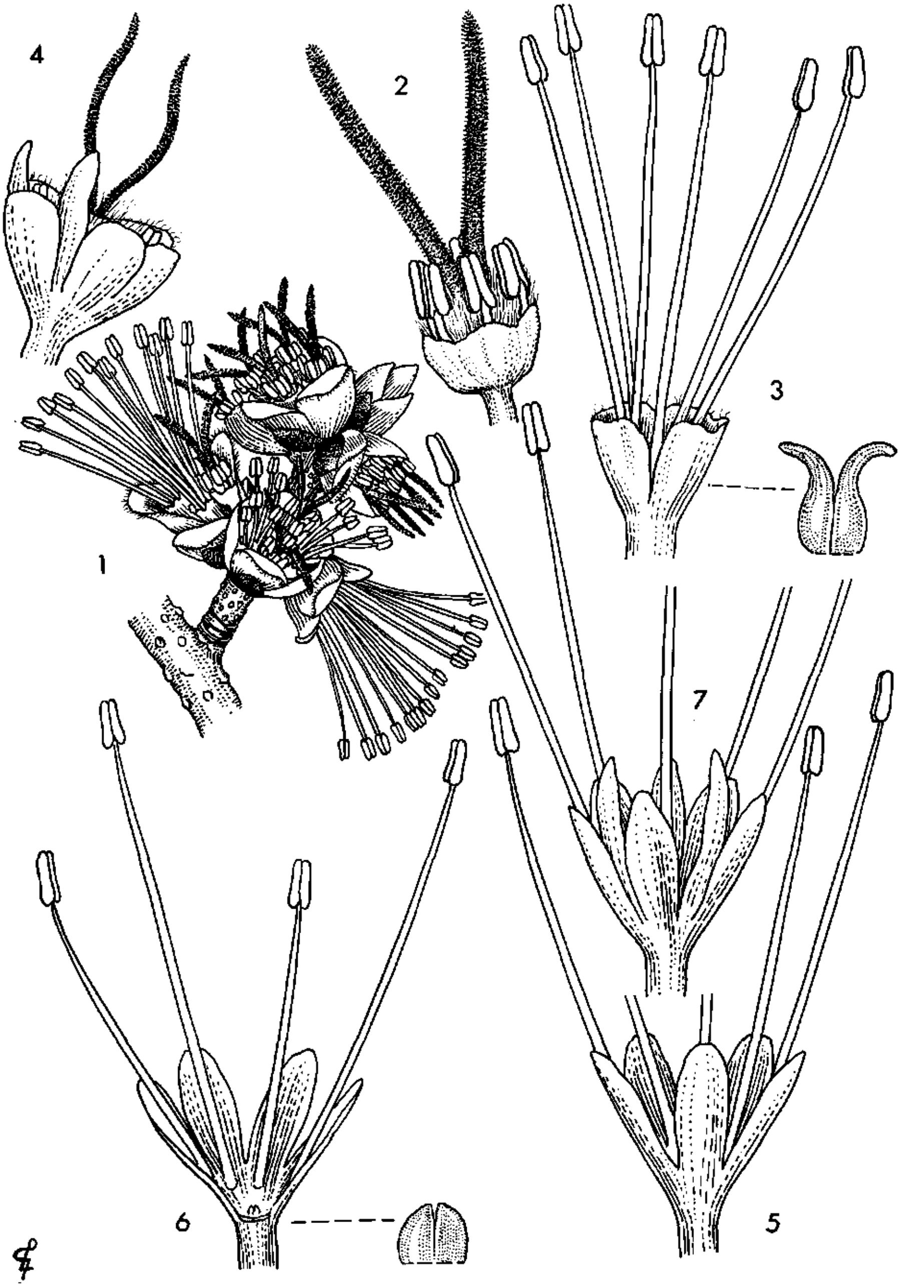


FIG. 27. *Acer saccharinum* L.: 1. branchlet with ♂, ♀ and androgynous infl. (2×); 2–7. fl. (6×): 2. ♀ fl., 3. ♂ fl.; abortive pistil (24×), 4. ♀ fl. with two petals, 5. ♂ fl.: sepals nearly free, 6. ♂ fl., longitudinal section: abortive pistil (24×), 7. ♂ fl. with three petals. (1–3. 'Eugeia', Wageningen; 4. 'Bowlespark', Wag.; 5–7. 'Schwerinii' Wag. B.G. no. 13276).

are clearly backward. The ♀ flowers also show some delay in development in relation to ♀ inflorescences. This delay was sometimes so strong that such androgynous inflorescences remained in the bud stage. It was observed that the ♀ flowers of androgynous inflorescences were mostly not located in the centre of the umbel. All ♂ flowers had a rather small abortive pistil, mostly with some development of the stigmas (see fig. 27.3). Although the picture of the studied monoecious trees of *A. saccharinum* highly corresponds with that of *A. rubrum*, it could not be concluded that only ♂$_{\text{II}}$ flowers were present. It may be possible that both types of ♂ flowers or even exclusively ♂$_{\text{I}}$ flowers occur, but the typical pattern of distribution of the ♂ and ♀ flowers within the single trees support the hypothesis that only ♂$_{\text{II}}$ flowers are present. However, it should be noted that only a rather low number of trees could be studied.

A. saccharinum only twice produced fruits during the observational period: in 1972 and 1974.

3. *Annual variations in the sex expression*

Several specimens at the Botanic Gardens and elsewhere at Wageningen were observed for several years. The results are listed in table 13. Old monoecious specimens of *A. saccharinum* showed a stronger tendency to flower completely ♀ than younger trees. From personal communications with Mr. Ruisch of the Laboratory of Plant Taxonomy it appeared that the isolated trees of the Bowlespark and Emmapark fruited abundantly in the past. The monoecious specimens of the same species largely corresponded in their yearly variations. This was especially the case with the two clonal specimens of *A. rubrum* (no. 1757), which flowered at nearly the same ratios of ♂ and ♀ flowers.

A remarkable observation was made during the autumn of 1969 and 1970 at Belmonte. After a rather dry summer all the ♂ specimens of both species dropped their leaves earlier than the monoecious and ♀ ones. It was further noticed that monoecious trees with a large portion of ♂ flowers in 1970 dropped the leaves on the upper branches of the crown (the part with the ♂ flowers!) much earlier than those on the lower branches during the previous autumn.

4. *Occurrence of bisexual flowers*

The observations of Hein (1907) and Kobendza (1953) about ☿ flowers on *A. saccharinum* could not be confirmed neither for the trees studied nor for herbarium specimens. On the contrary, as found by Haas (1933), ☿ flowers were produced on some *A. rubrum* specimens. In 1969 and 1970 some (♀) flowers of no. 1757 I and II shed pollen (see fig. 26,2). It was also noticed that the stamens of all ♀ flowers of these specimens had relatively large filaments. However, in 1971 ☿ flowers were also observed on 'Sanguineum' (no. 7809). The stamens of these flowers had the same short filaments as normal ♀ flowers of this specimen. In both cases the pollen was germinated experimentally. The ☿ sex expression of these flowers seemed to be caused by relatively high temperatures, combined with a low relative humidity. In herbarium collections ☿ flowers were found once: Gamble 30535, cultivated (K).

ABLE 13. Sex expression observed on specimens of section *Rubra* in the Botanic Gardens and elsewhere at Wageningen.

species cultivar (location)	garden number	sex expression (ratios)						
		1967	1968	1969	1970	1971	1972	1974
1. *rubrum*	1757-I	♂/♀ (10/1)	♂/♀ (5/1)	♂/♀ (1/2)	♂/♀ (50/1)	♂/♀/☿ (100/10/1)	♂/♀ (100/1)	♂/♀ (100/1)
	1757-II	♂/♀ (10/1)	♂/♀ (5/1)	♂/♀ (1/2)	♂/♀ (50/1)	♂/♀/☿ (100/10/1)	♂/♀ (100/1)	♂/♀ (>100/1)
'Sanguineum'	7809	♀	♀	♀	♀	♀/☿ (5/1)	♀	♀
'Scanlon'	18077	♀	♀	♀	♀	♀	♀	♀
'Schlesingeri'	7811	♂	♂	♂	♂	♂	+	
'Schlesingeri'	11472	♂	♂	♂	♂	♂	♂	♂
'Taranto'	15724	–	♂	♂	♂	♂		
'Tilford'	15922	♀	♀	♀	♀	♀	♀	♀
1. *saccharinum*								
	11716	♀	♀	♀	♂/♀ (1/50)	♀	♂/♀ (1/5)	♂/♀ (1/10)
	12288	♂	♂	♂	♂	♂	♂	♂
	12432	♀	♀	♀	♂/♀ (1/100)	♀	♂/♀ (1/3)	♂/♀ (1/5)
'Asplenifolium'	12425-I	♀	♀	♂/♀ (1/20)	♂/♀ (1/1)	♀	♂/♀ (1/10)	♂/♀ (1/50)
'Asplenifolium'	12425-II	♀	♀	♂/♀ (1/10)	♂/♀ (5/1)	♀ ♀	♂/♀ (1/10)	♂/♀ (1/100)
'Elegant'	7810	♂	♂	♂	♂	♂	♂	♂
'Lutescens'	13167	♂	♂	♂	♂	♂	♂	♂
'Pulverulentum'	796	♀	♀	♀	♂/♀ (1/100)	♀	+	
'Schwerinii'	13276	♂	♂	♂	♂	♂	♂	♂
'Laciniatum'	797	♀	♀	♀	♂/♀ (1/3)	♀	+	
(Bowlespark)			♀	♀	♀	♀	♀	♂/♀ (<1/1000)
(Emmapark)			♂/♀ (1/100)	♀	♂/♀ (1/100)	♀	♀	♀
(Eugeia)				♂/♀ (1/10)	♂/♀ (1/3)	♂/♀ (1/10)	♂/♀ (1/3)	

– no flowers + cut down

5. *Relation between the number of stamens and sex expression of flowers in A. saccharinum*

HEIN (1907) reported that ♂ flowers had 4–7 stamens, while ♀ flowers only had 1–5 stamens. This was further studied on two monoecious specimens: 'Laciniatum' no. 797 and the tree near Eugeia. The results are shown in table 14. The counts did not nearly comprise 1 per mille of all flowers of the corresponding trees. The results largely vary from those of HEIN. Rather small variations between ♂ and ♀ flowers were noticed. All ♂ flowers had a rudimentary pistil. These pistils were slightly larger in 'Laciniatum'.

TABLE 14. Variations in the number of stamens between ♂ and ♀ flowers of two *Acer saccharinum* specimens.

specimen location	number of stamens						
	3	4	5	6	7	8	average
'Laciniatum' Wag. B.G. 797							
♂ flowers	2	2	17	53	41	4	6.2
♀ flowers	–	2	32	42	17	1	5.8
Eugeia (Wageningen)							
♂ flowers	–	3	75	44	7	–	5.4
♀ flowers	–	4	84	26	1	–	5.2

6. *Degree of variability in the section*

The portion of monoecism in *A. rubrum* is probably rather low and variable, while monoecious flowering specimens may sometimes be entirely lacking. Only one type of androgynous inflorescences was found. Monoecism occurs much more frequently in *A. saccharinum*. The portion of ♂ specimens in the populations of these species seems variable; e.g. HEIN (1907) did not notice ♂ specimens. In contrast with *A. rubrum* no trees were found which produced exclusively ♀ flowers in all observational years. Herbarium specimens of *A. saccharinum* predominantly had ♂ or ♀ flowers. This may be due to the occurrence of exclusively ♀ flowers on the lowest branches of monoecious specimens.

The occurrence of ♂$_{\text{I}}$ flowers besides ♂$_{\text{II}}$ flowers could not be established.

The few available herbarium specimens of *A. pycnanthum* from Japan had ♂ or ♀ flowers.

VIII. Section Ginnala

1. *Introduction and literature*

From this small section specimens of *A. ginnala* and *A. tataricum* were studied at the Wag. B. G. and occasionally at the Gimborn Arb. and Zuiderpark. In literature the species are described as monoecious. HAAS (1933) observed about thirty specimens of *A. tataricum*. He found as many specimens with inflorescences of type B as specimens with type D.

2. *Results of observations*

The flowering times of both species nearly coincided at the beginning of June, about 4–6 weeks after the unfolding of the leaves. The rather large inflorescences had the same structure as those of *A. platanoides* (type II, see 2.3.1).

With one exception (see next paragraph) all the studied specimens had the same flowering types during all the years of observations. At Wageningen *A. ginnala* no. 12481, and *A. tataricum* no. 795 produced inflorescences of type B. *A. ginnala* no 8330, no. 12278 and no. 15000 and *A. tataricum* no. 15495

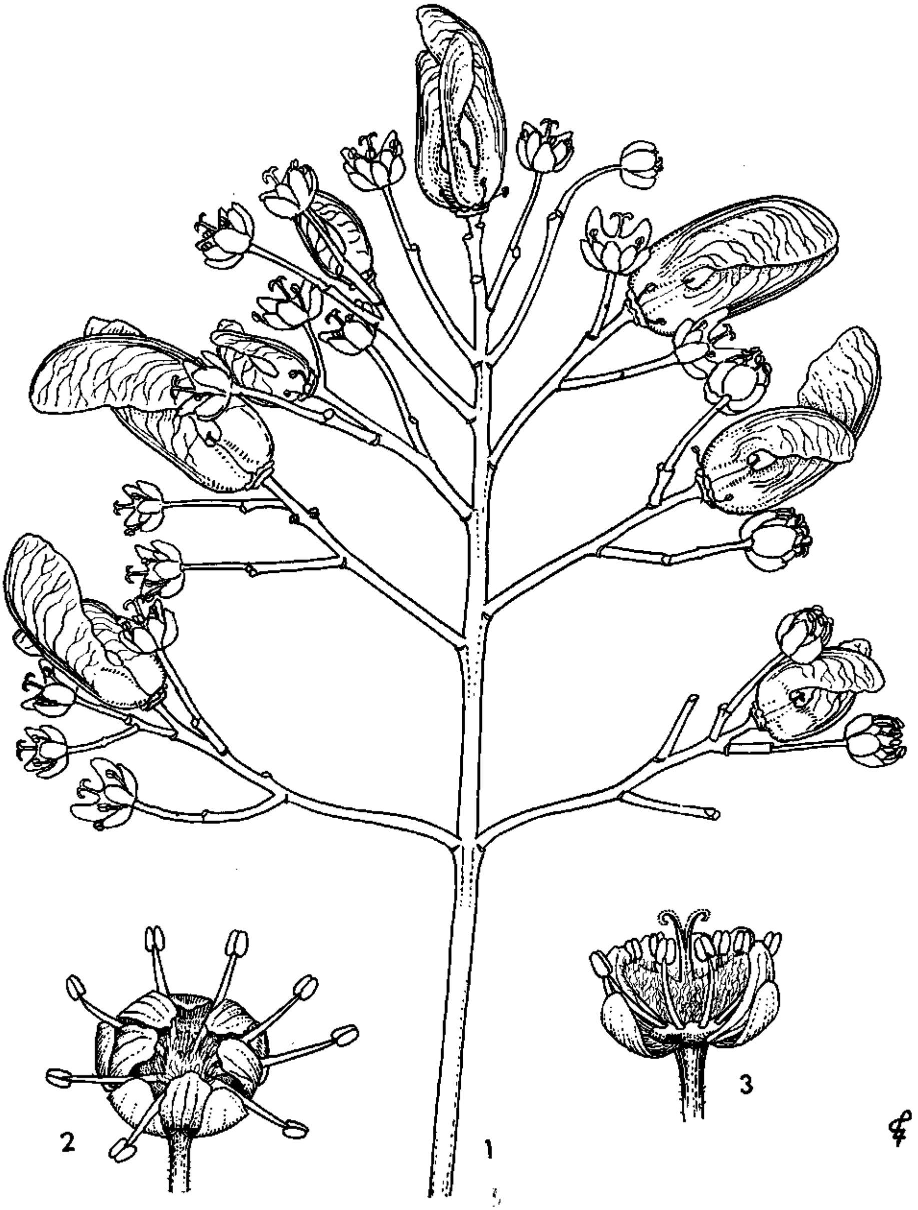


FIG. 28. *Acer ginnala* Maxim.: 1. infl. showing a second phase of ♀ fl. in the largest part of the secondary axes ($1^1/_2\times$); 2. ♂$_{\text{II}}$ fl. ($4\times$); 3. ♀ fl., part of perianth removed ($4\times$). (Wag. B.G. no. 12481).

represented type C, occasionally mixed with type D.

The inflorescences of *A. ginnala* no. 8330 showed a clear demarcation between the three phases. This is shown in fig. 2. The ♂$_{\mathrm{I}}$ flowers had already dropped when the ♀ flowers opened. The stigmas of the latter were withered before the ♂$_{\mathrm{II}}$ flowers started anthesis. In most years the successive stages of ♂ and ♀ flowers occurred rather simultaneously on the whole shrub and only few fruits were produced.

3. *Occurrence of a second ♀ phase*

In 1969 and 1970 this phenomenon could be observed on *A. ginnala* no. 12481. In the first year it was only found on the east side of the shrub. In 1970 on the east and west sides. The ♀ flowers of the second phase appeared at a time when other inflorescences were still in the ♂$_{\mathrm{II}}$ phase. Even parts of the inflorescences with this second phase of ♀ flowers produced ♂$_{\mathrm{II}}$ flowers at the same time. Fig. 28 shows an inflorescence with the phenomena described. A number of these inflorescences of type G had little or no fruit set after the first ♀ phase, but in general no relation was found between the number of fruits of the first ♀ phase and the occurrence of a second ♀ phase.

Although pollination of the ♀ flowers of the latter phase was possible no fruits were obtained. In 1970 some inflorescences produced ♂ flowers after the second ♀ phase: type K.

IX. Section Lithocarpa

A. Series Lithocarpa

The species of this series are dioecious. The inflorescences developed from leafless lateral buds. The ♀ flowers lack stamens, while the abortive pistil of ♂ flowers are very small and mostly covered with a tuft of hairs. Only herbarium specimens were studied.

B. Series Macrophylla

1. *Introduction and literature*

Of the single species of this series, *A. macrophyllum*, only two living specimens could be studied. One large tree of about 60 years old was present in the Wag. B.G. and another tree of about 40 years old in the Zuiderpark. A study of flowering of this species was also made on herbarium specimens from natural stands.

In literature no special notes were found on the flowering of this species, which was always described as monoecious.

2. *General observations on flowering*

Flowering started at Wageningen in April before the unfolding of the leaves. The inflorescences appeared from mixed terminal and lateral buds. Both specimens studied started anthesis in all years of observations with a ♂$_{\mathrm{I}}$ phase.

FIG. 29. *Acer macrophyllum* Pursh.: Infl. (natural size); 1. duodichogamous infl. (flowering type C) at the end of the ♂$_1$ phase, stigmas of ♀ fl. become visible (May 5, 1969); 2. small protogynous infl. (flowering type B) starting anthesis during ♀ phase of the tree (May 9, 1969). (Wag. B.G. no. 1779).

Within the trees there was a rather sharp division between the ♂$_{\mathrm{I}}$ and the ♀ phase and an overlap between the ♀ and ♂$_{\mathrm{II}}$ phase. Fig. 29,1 shows an inflorescence at the end of the first ♂ phase and fig. 29,2 a protogynous inflorescence, which started flowering in the ♀ phase of the tree. The large inflorescences of both specimens had the flowering type C. Some small inflorescences could show types D and B, depending on the moment at which flowering started. There was a conspicuous difference between the aborted pistils of ♂$_{\mathrm{I}}$ and ♂$_{\mathrm{II}}$ flowers (see fig. 30 and the notes in 4.6).

Out of a number of 96 herbarium specimens, collected at natural stands in the Western part of the United States, 56 had a ♂ and 40 a ♀ start of flowering.

The occurrence of ♂ specimens seems unlikely.

3. *Occurrence of bisexual flowers*

In 1969–1971 it was observed at Wageningen that the locules of the anthers of several ♀ flowers opened and pollen was shed (see fig. 30,3). This took place at the end of the ♀ phase, while ♂$_{\mathrm{II}}$ flowers were already open.

The stigmas of these bisexual flowers were sometimes so far bent, that they touched the locules of the hairy ovary, which were covered with pollen. In some tests the pollen of the ☿ flowers failed to germinate, while at the same time pollen of the ♂$_{\mathrm{II}}$ flowers germinated very well. From microscopic studies of the pollen it could be concluded, that besides some small variation in colour, the pollen of ☿ flowers had a variable diameter, which was smaller than that of the ♂ flowers.

The weather conditions at the moment of observation of these ☿ flowers were marked by relatively high temperatures and a low humidity.

Some herbarium specimens from natural stands also showed these ☿ flowers: Vancouver Islands and Simago, Wash. B.C., Lyall s.n., (K); Victoria, Wash. B.C., Fletcher 146 (BM); Columbia river, Wash. B.C., Surksdorf s.n. (BM); Santa Clara County, Cal., Carter 1041 (BM), Mendocino County, Cal., Hutchinson 2408 (BM).

Because at the time when some ♀ flowers became ☿, ♂$_{\mathrm{II}}$ flowers were present for pollination, the pollen of these ☿ flowers, fertile or not, will be superfluous. In the opinion of the author this bisexuality is nothing else than a remnant of the past.

X. Section Negundo

Both series of this section, *Negundo* and *Cissifolia*, are dioecious. The ♀ flowers normally lack stamens. HALL (1954) found some ♀ specimens of *A. negundo*, which produced flowers with 1–3 stamens. FRASER (1912) reported about 'induced hermaphroditism' in *A. negundo*. He found near Weston, Ontario (Canada), a tree with normal ♀ flowers except on one branch. By some accident this branch had been partly split from the trunk. On this single branch the flowers were hermaphrodite showing (0–)3–4(–5) stamens. No data were given about a probably pollen shed. The structure of the inflores-

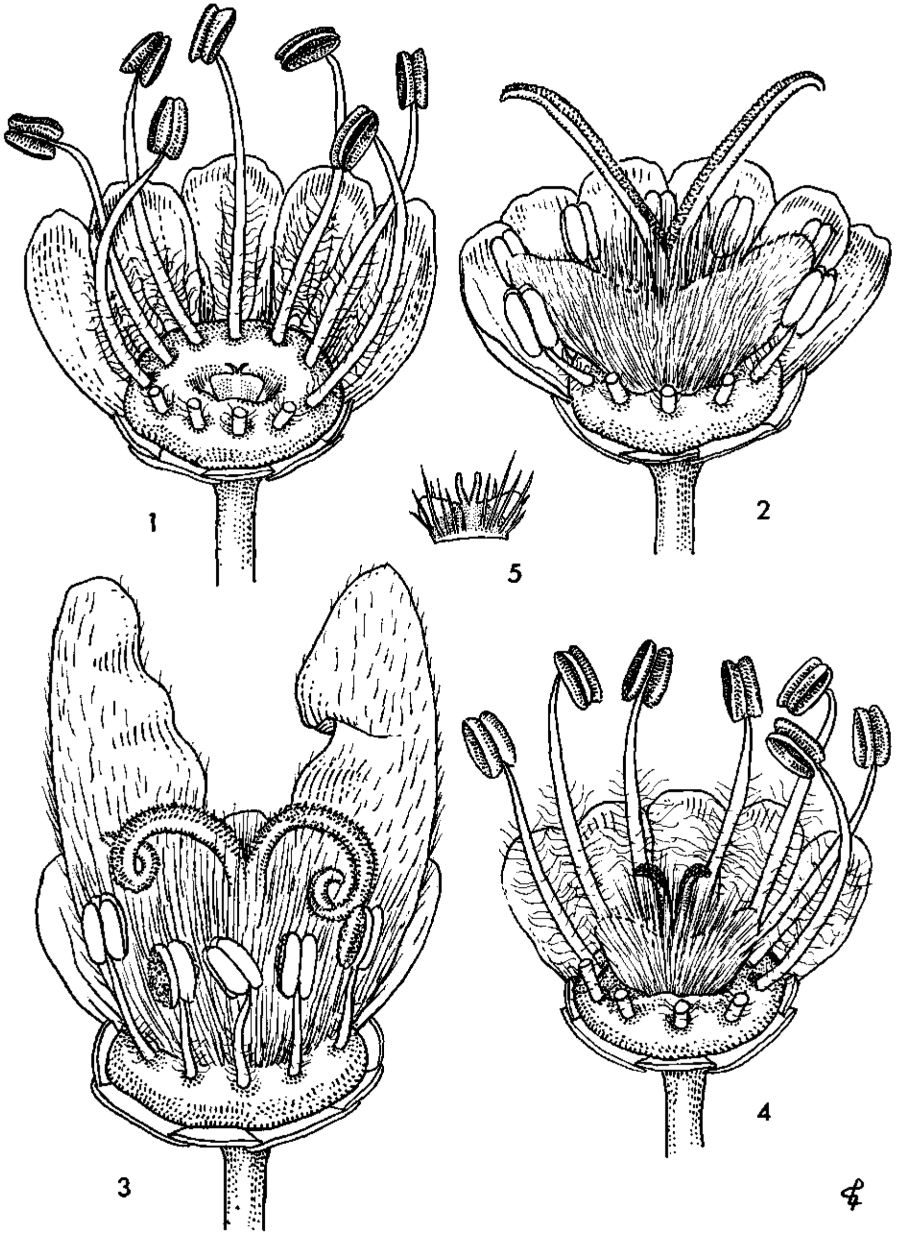


FIG. 30. *Acer macrophyllum* Pursh.: 1–4. fl., part of perianth and androecium removed (6×): 1. ♂$_{\mathrm{I}}$ fl., 2. ♀ fl., at the beginning of anthesis, 3. ☿ fl.: pollen release at the end of the receptive period (protogyny), 4. ♂$_{\mathrm{II}}$ fl.: abortive pistil hairy; 5. abortive pistil of ♂$_{\mathrm{I}}$ fl., scarcely hairy at the basis (12×). (Wag. B.G. no. 1779).

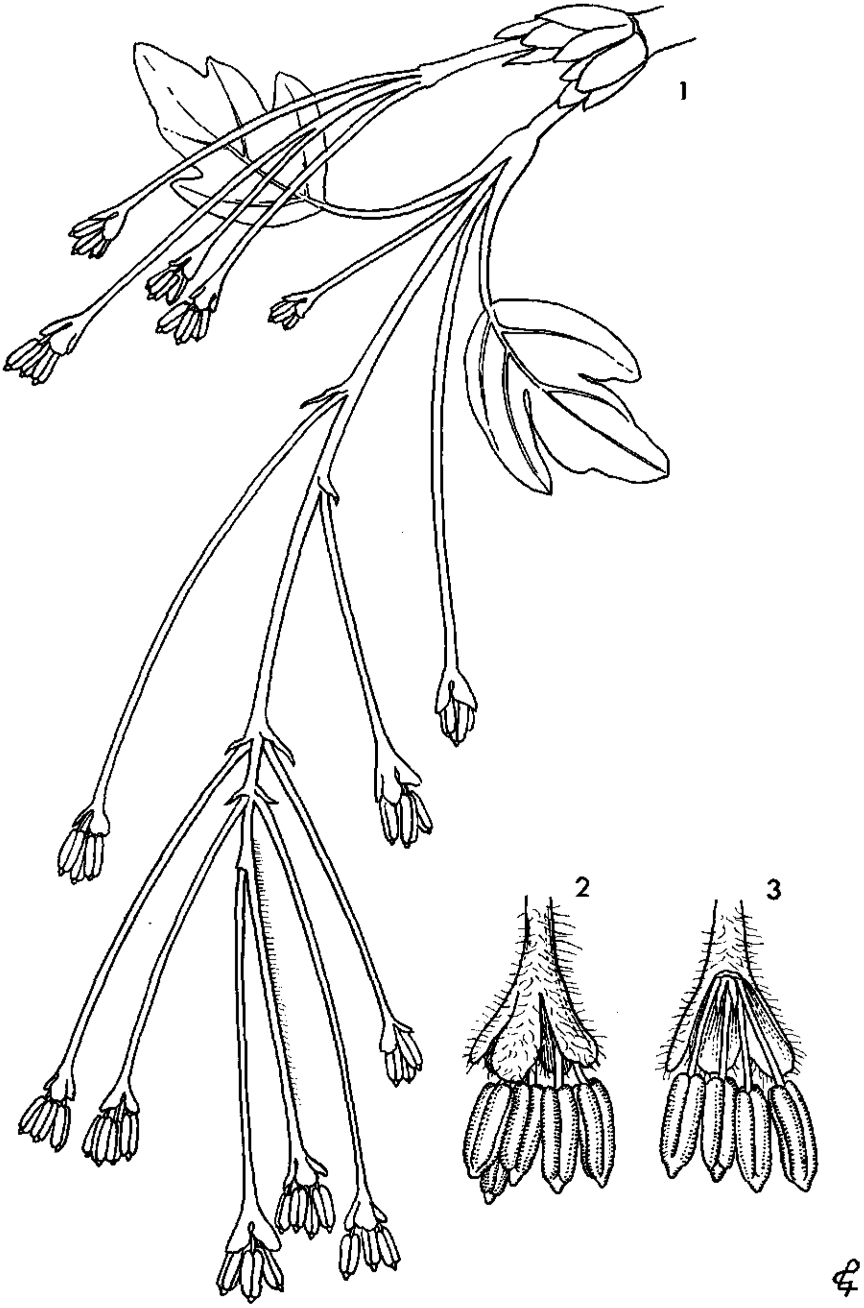


FIG. 31. *Acer negundo* L.: Male: 1. branchlet (5×); 2. fl. (10×); 3. fl., part of calyx removed: rudimentary pistil, two unconnate carpels. (var. californicum (T. & G.) Sargent Wag. B.G. no. 13166).

cences on that branch also differed from normal racemose ♀ inflorescences and more or less resembled that of ♂ inflorescences. The flowering of the tree concerned was not observed in later years.

The flowering of *A. negundo* started between the end of March and mid April before the unfolding of the leaves. A ♂ inflorescence is shown in fig. 31. The ♀ inflorescences develop very slowly, but it was observed that the stigmas of the flowers were already receptive at a time when the flowers were seemingly still in bud (see fig. 32,1). The ♀ flower enlarged during the receptive period, which could last up to three weeks. Three-weeks-old flowers are shown in fig. 32,3. They differ in the size of all pistil parts, while the sepals still have the same size as at the onset of anthesis.

The species *A. cissifolium* and *A. henryi* of series *Cissifolia* started flowering before the unfolding of the leaves at the beginning of May. The inflorescences developed from lateral buds. Occasionally ♂ specimens produced three inflorescences from one lateral bud. *A. henryi* dropped the rather small whitish petals of the flowers very early, sometimes already before anthesis.

XI. Section Glabra

A. Series Glabra

The single species of this series, *A. glabrum*, was only studied from herbarium specimens. SARGENT (1891) reported about the sex expression that this species usually had ♂ and ♀ trees. PAX (1902) considered the species as monoecious, REHDER (1927) and OGATA (1967), as monoecious or dioecious.

Of a number of 51 specimens from natural habitats 36 had ♂ inflorescences, 4 had ♀ inflorescences and 11 had inflorescences of type B, partly mixed with type F. The specimens with ♂ inflorescences never had fruit stalks of previous years. The only exception may be: Nelson 5786 (P): $♂_{(II?)}$ flowers and one old fruit stalk. These observations agree with those on *A. rubrum*.

One specimen, however, confused this picture. In the collection of cultivated plants at the Kew Herbarium I found some sheets of *A. glabrum* from a tree of the Botanic Gardens under garden number 205 and association number E.N. 517: 95AA. Some sheets, collected in 1963, had exclusively ♂ inflorescences and no old fruit stalks, while other sheets collected in 1961 had numerous fruits and old fruit stalks. In the autumn of 1969 the tree concerned was observed in the garden. A few fruits were present in the upper part of the crown. On inquiry it became obvious that originally there were two specimens with garden number 205, but it was not known when the second tree was lost. The supposition that the lost tree was a ♀ specimen was overthrown by a second observation of the tree in 1972. Of two main branches one had several fruits on inflorescences which represented the types A and B, while the other had neither fruits nor fruit stalks of previous years, but several scars of dropped inflorescences. No doubt these marks originated from ♂ inflorescences, because this species has a strong tendency to parthenocarpy. A closer examination of the ♂ flowers of the herbarium specimen showed that the abortive pistils had the same size and stage of development as those from ♂ inflorescences of other specimens. Finally it could be established that the '♂ branch' was not grafted.

This single observation undermined the previous hypothesis of the sex expression of this species and needs farther study, especially of the natural habitats of this species.

B. Series Arguta

The species of this series are dioecious. The ♂ trees produce their inflorescences only from predominantly leafless, lateral buds. The inflorescences on ♀ trees mainly develop from mixed terminal buds. On vigorous shoots they also appear from, often leafless, lateral buds.

Since ♂ specimens do not form more pairs of bud scales than ♀ specimens, the development of a pair of leaves before floral initiation in ♀ specimens could indicate an earlier onset of floral initiation in ♂ trees during the summer. This supposition further strengthened by the presence of more flowers in the inflorescences of ♂ trees, as compared to the ♀ trees, could unfortunately not be examined owing to the scarcety of living specimens in the Dutch collections.

XII. Section Integrifolia

A. Series Trifida

The species of this section, described as monoecious, were studied from herbarium specimens.

The rather large inflorescences mainly developed from mixed terminal buds. Flowering types B, C and D were found.

B. Series Pentaphylla

Of the single species of this section, *A. pentaphyllum*, only specimens of the type collection could be studied: Muli Kingdom, Szechuan, China, J. F. Rock 17819 (BM, E, K, P, W). The inflorescences represent type B.

XIII. Section Indivisa

The single species of this section, *A. carpinifolium*, is dioecious. The inflorescences are developed from mixed terminal and lateral buds. The flowers of the drooping racemes had long thin pedicels, showing a tendency to wind pollination.

Flowering started simultaneously with the unfolding of the leaves.

A. carpinifolium is the single dioecious species studied, which had ♀ flowers with rudimentary stamens. These stamens, 3–6 per flower, were differently sized. The anthers never contained pollen.

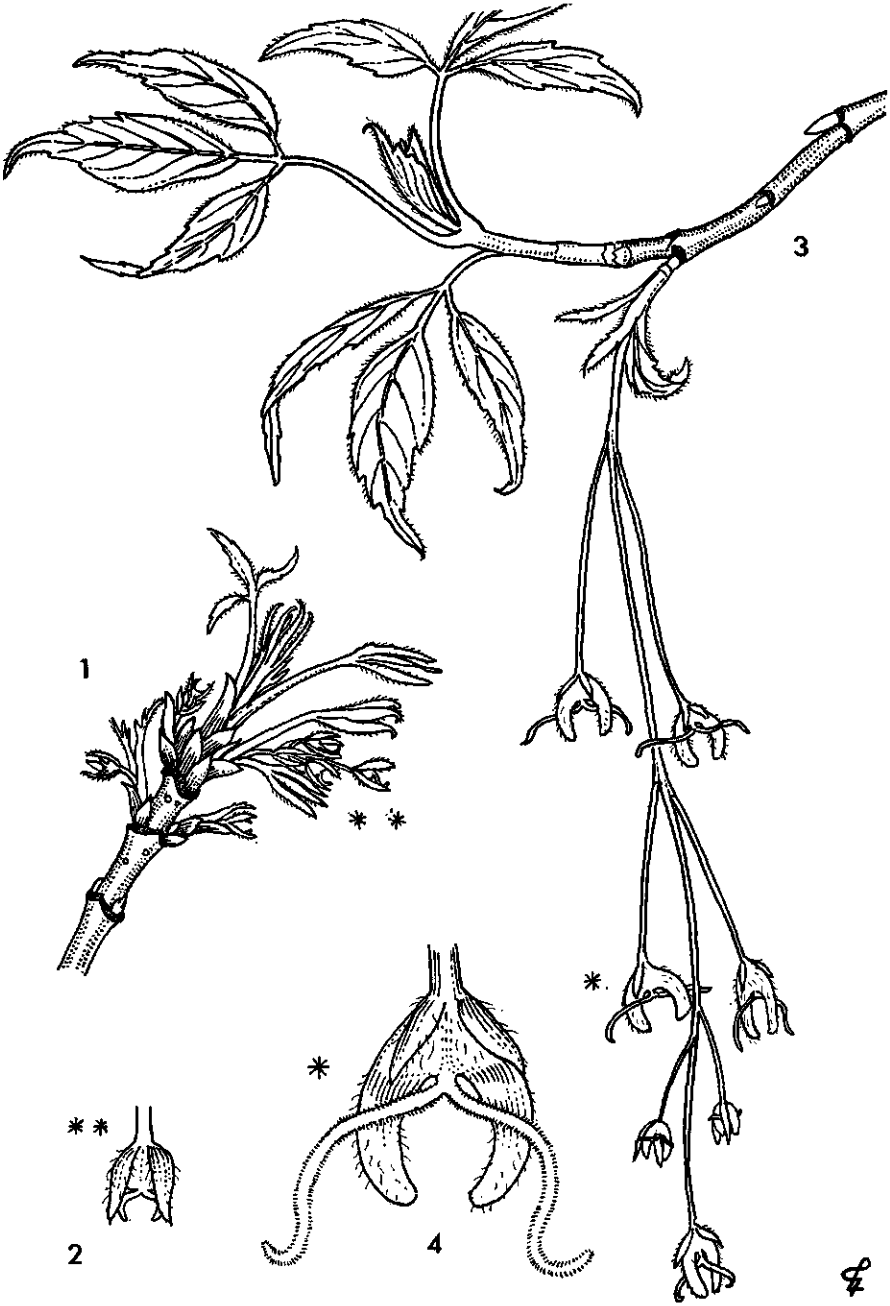


FIG. 32. *Acer negundo* L.: Female: 1. branchlet at the beginning of anthesis (April 2, 1969) (2 ×); 2. fl. (6 ×); 3. branchlet with receptive fl. (April 21, 1969) (2 ×); 4. fl. (6 ×). ('Argenteocinctum' Wag. B.G. no. 15920).

XIV. **Section Hyptiocarpa**

Of this section the sex expression of the species *A. garrettii* (syn. *A. decandrum*) and *A. laurinum* was studied from herbarium specimens. Fang (1939) described *A. garrettii* as dioecious. Bloembergen (1948) observed that the inflorescences of *A. laurinum* were either ♂ or ♀, but rarely with flowers of the other sex.

The inflorescences had, depending on their size, a cymous (*A. laurinum*) or nearly racemose structure (*A. garrettii*). They were developed from leafless lateral buds on leafy or leafless branches. Especially *A. laurinum* showed a large variation in the size of the inflorescences and the ♂ flowers.

Most specimens had ♂ or ♀ inflorescences. Two specimens of *A. garrettii* had ♂$_{II}$ flowers (type F): Tam Dar, Tonkin, Petelot 5969 (P) and Paak Shek Shan, Hainan, W.T. Tsang 633 (P). Two protogynous specimens of *A. laurinum* were noticed: G. Gede, Java, Fornaer 106, (K, L) and Indonesia, Anonymous s.n. (BM). Protandrous inflorescences were produced by one specimen of the latter species: Haviland, Borneo, Anonymous 2092 (L). These scarce data give an incomplete picture of the variability in this section. A considerable number of the specimens will probably be dioecious, while the sex expression of the monoecious specimens may strongly depend on environmental conditions. The proportion of ♂ flowers on the latter specimens may predominate under unfavorable conditions.

3.4. SOME NOTES ON MONOECISM IN RELATED TAXA

Many data on monoecism in higher plants were collected to find out correlations with this specialisation in *Acer*. Several papers on this subject were reviewed by Heslop-Harrison (1957) and Napp-Zinn (1967). It was concluded that monoecism comprises more or less independently developed specialisations in the reproductive system, which often show a close agreement in their reaction to varying environmental conditions (e.g. temperature, daylength). At the same time various monoecious taxa showed rather similar reactions to treatment with phytohormones (auxins, cytokinins, gibberellins). Most points of contact for comparison and better understanding of the sex expression in *Acer* were present in related taxa, which may have undergone similar developments during their evolution or at any time already had monoecious ancestors.

Knuth (1904) and Hardin (1956) reviewed some papers on the sex expression of *Aesculus hippocastanum* L. (*Hippocastanaceae*). Conflicting notes were found about the appearance of the ☿ flowers during anthesis and their position in the inflorescences. Some authors observed a start of anthesis with ☿ flowers or a limitation of these flowers to the lowest cincinni. Others noticed an onset of flowering with exclusively ♂ flowers and a distribution of ☿ flowers in the higher parts of the inflorescences. On the basis of studied herbarium specimens Hardin concluded that both possibilities occurred.

BENSELER (1969) studying the reproduction of *Aesculus californica* (Spach) Nutt. found that flowering started with ♂ flowers. When a relatively high number of ☿ flowers were produced, these flowers appeared earlier during the flowering period. He also found that the population in the coastal areas of California, which have a more humid and milder climate, produced more ☿ flowers than the populations in most other areas. In coastal areas 75 per cent of the inflorescences showed one or more ☿ flowers. Specimens without completely ♂ inflorescences were rarely observed (0.2%), while in all areas studied ♂ flowering specimens were also only occasionally found (0.4%). The mean ♂/☿ ratio was about 30: 1. MEEHAN (1891) noticed the same ratio for *Aesculus parviflora* Walt. As reported earlier for *Aesculus hippocastanum* (KNUTH, 1904) BENSELER noticed a protogynous sex expression of the ☿ flowers of *Aesculus californicum.* HOFFMANN (1871) observed that seedlings of *Aesculus hippocastanum* were only ♂ flowering in the beginning of their generative stage.

LIU (1954) studied the sex expression of *Litchi chinensis* Sonn. (*Sapindaceae*). She noticed that all studied varieties started anthesis with a ♂ phase of flowers followed by ♀ flowers and finally by a second phase of ♂ flowers. Within single inflorescences no overlap of phases was observed. Nevertheless overlap occurred between various inflorescences of a specimen. During a second flowering period anthesis often started with a ♀ phase of flowers. The morphologic differences between the ♂ flowers of both phases were very similar to those described for *Acer.*

The present author observed the flowering of living specimens of *Aesculus, Deinbollia* and *Koelreuteria* (the latter both *Sapindaceae*) and of the second genus of *Aceraceae, Dipteronia.* The only living specimen available of *Dipteronia sinensis* Oliv. (Gimborn Arb.) showed a ♂-♀-♂ sequence of phases during all years of observations. This condition was mostly also noticed in the herbarium specimens studied. At the Wag. B.G. specimens of *Aesculus* × *carnea* Hayne, *A. glabra* Willd., *A. hippocastanum* L. and *A. octandra* Marsh mostly started flowering with ♂ flowers. Those specimens which produced their ☿ flowers first, usually started flowering with some ♂ flowers in at least one of the following years. On a single inflorescence the ☿ flowers appeared rather simultaneously, without interrupting ♂ flowering on cincinni without ☿ flowers. The number of ☿ flowers per inflorescence depended on the size of the inflorescences and their position in the trees and also showed variations between the studied specimens of a species. The inflorescences more on the periphery of the tree produced more ☿ flowers than those more inside. Special observations were made on *Aesculus hippocastanum* 'Umbraculifera' (no. 14361), a cultivar with a very compact globular crown. The strongly shaded inflorescences inside the crown only produced ♂ flowers, while those on the periphery had 10 or more ☿ flowers.

Similar observations were made on *Aesculus parviflora* Walt. (no. 1074). The production of ☿ flowers on this specimen also seemed to be strongly dependent on environmental conditions. During the five years of observations ☿ flowers only appeared after some cool days during the flowering period. Most of the

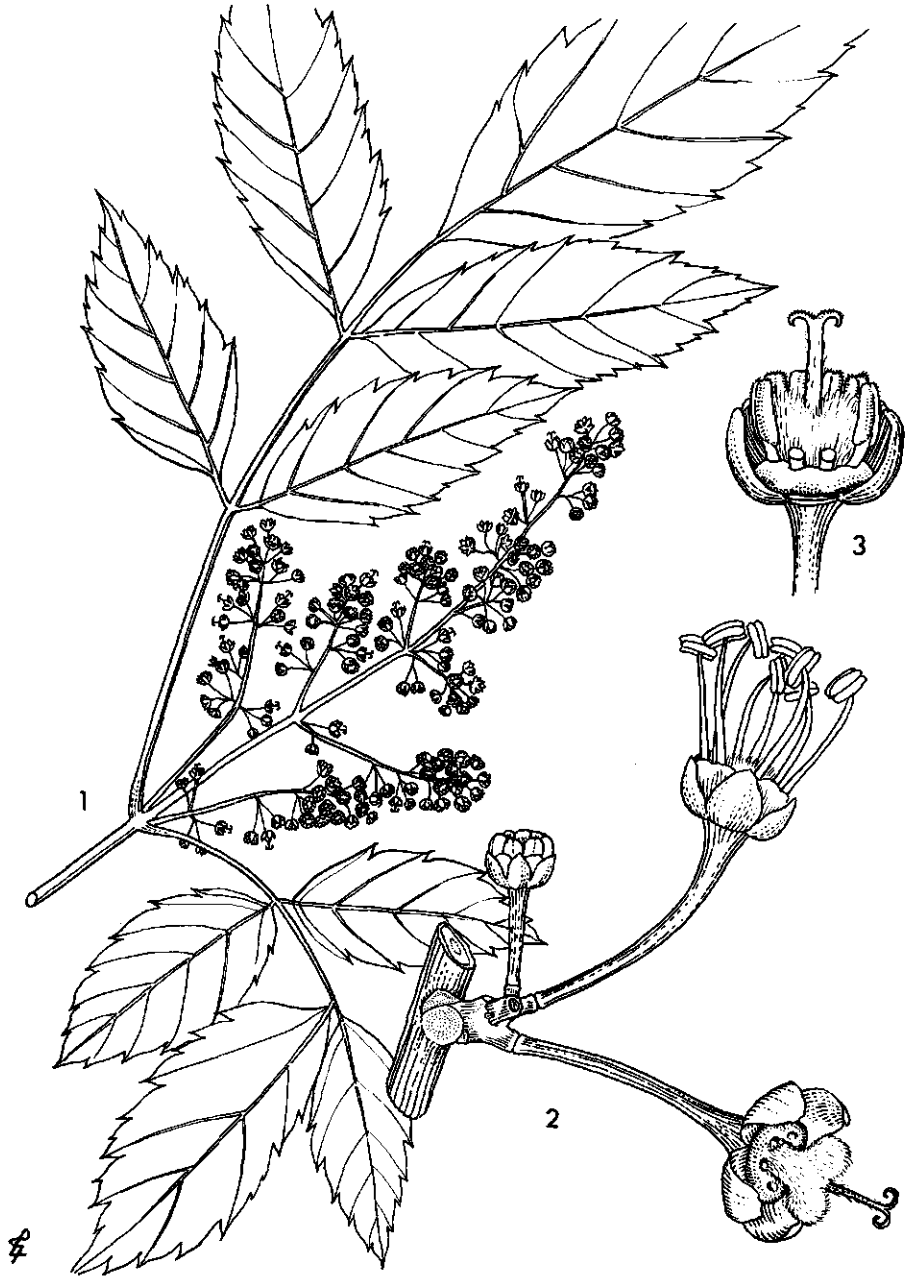


FIG. 33. *Dipteronia sinensis* Oliv.: 1. flowering branchlet during ♀ phase ($^5/_6\times$); 2. cincinnus during $♂_{II}$ phase, articulation of the pedicels on the place of future abscission (8 ×); 3. ♀ fl. (part of perianth removed), disc extrastaminal (8 ×). (Gimborn Arb.).

☿ flowers were present on the largest inflorescences on the less shaded parts of the shrub. In 1974, after a very cool period, part of these inflorescences produced a second phase of ☿ flowers. At the same time most of the remaining inflorescences showed their first ☿ phase.

Two specimens of *Koelreuteria paniculata* Laxm. (nos. 1080 and 1083) were observed in 1970. Both showed a ♂–♀–♂ sequence, while ♀ flowers were only produced in part of the inflorescences. Some inflorescences, which started anthesis relatively late, flowered protogynously.

A specimen of *Deinbollia grandifolia* Hook. f. (Ivory Coast, Oldeman 139, no. 11) was studied in a greenhouse of the Wag. B.G. The ♂–♀–♂ sequence did not show overlap of the phases within a single inflorescence.

Studying material of *Sapindaceae* in Herbarium Vadense (WAG) the present author noticed that anthesis of taxa with large multiflorous inflorescences, such as are found e.g. in *Allophyllus, Aphania, Aporrhiza, Deinbollia* and *Radlkofera*, predominantly started with ♂ flowers, while all inflorescences showed a phase with ♀ flowers. Small overlaps were only noticed between the ♀ and ♂$_{\mathrm{II}}$ phase. The abortive pistil of ♂$_{\mathrm{II}}$ flowers in most cases larger and further developed than those of ♂$_{\mathrm{I}}$ flowers.

3.5. Discussion and conclusions

The variability of the sex expression in *Acer* was studied at three levels: individuals, species and the genus as a whole.

3.5.1. *Sex expression of individual plants*

For the sex expression of a single plant four main possibilities are distinguishable.

1. **Protandry** (including duodichogamy). Anthesis of the inflorescences starts with a phase of ♂ flowers followed by one with ♀ flowers (flowering type D). The ♀ phase may be followed by a second phase of ♂ flowers (type C, duodichogamy). All inflorescences may show the same flowering type, but a single plant may also produce two or more flowering types (e.g. types D and E, C and D or C, D and E).

The change to a phase with flowers of another sex generally occurs simultaneously within the whole tree. In consequence small inflorescences frequently flower during fewer phases than larger ones. An asynchronous change of phases may be found on trees which also develop inflorescences on long shoots of the previous year. Anthesis on such branches often starts some days later and protogynous inflorescences may sometimes be noticed (type B).

Occasionally a small part of the inflorescences of a tree may produce a second phase of ♀ flowers (types J and L) or lack ♀ flowers between the two ♂ phases (type G).

In successive years individuals always show the same flowering type or combination of flowering types, but annual variations may often occur. Particularly environmental conditions just before and during anthesis seem to influence the length of the ♀ phase. It was noticed that relatively high temperatures reduced the number of ♀ flowers. Variation in time of floral induction must also be involved (see chapter 4).

The mean size of the inflorescences shows yearly and local fluctuations, which may cause a variation in the number of phases realised and the mutual frequency of the flowering types. This variability may also lead to fruiting in alternate years. Despite the asynchronous flowering of ♂ and ♀ flowers it was noticed that isolated trees always produced fruits as a consequence of self-pollination (geitonogamy).

2. **Protogyny.** A phase of ♀ flowers followed by one with ♂ flowers (type B). One of both phases may lack in relatively small inflorescences (types A and F). The change from the ♀ to the ♂$_{II}$ phase usually occurs simultaneously in the whole tree. There are small overlaps of both phases within single inflorescences particularly if low temperatures lengthen the stigmatic receptivity of ♀ flowers.

A somewhat later start of anthesis may be shown by inflorescences on long shoots of the previous year. This mostly does not influence the length of the ♀ phase of these inflorescences. Consequently the ♂$_{II}$ phase will appear one or a few days later in these inflorescences than elsewhere on the tree.

A number of inflorescences sometimes produce some ♂$_{I}$ flowers (type C) as a consequence of special environmental conditions and the genetic constitution of the corresponding taxa.

Occasionally a second ♀ phase was noticed followed by ♂ flowers (types G and K respectively). Protogynous flowering individuals mostly show only small local and yearly variations in their sex expression

3. **Male.** This possibility concerns genetically ♂ and ♂ flowering individuals. The latter are essentially monoecious and mostly protandrous. Observations over a long period will confirm this monoecism, but environmental conditions may reduce the incidence of monoecious flowering. Male flowering specimens may especially be found in taxa with rather small, racemose inflorescences.

4. **Female.** This relates to ♀ individuals and ♀ flowering individuals. The latter are mostly essentially protogynous and occur in taxa with relatively small inflorescences. A few essentially protandrous flowering taxa show ♀ flowering specimens (see 3.5.3). As stated for ♂ flowering specimens, environmental conditions are of importance for the frequency of years with a monoecious flowering.

3.5.2. *The effects of variable sex expression within the species*

The best way of investigating the mutual relationships of monoecious flowering individuals with regard to their reproduction would be to study populations in their natural habitats and to carry out breeding experiments. In this connection only few data have been published, while the present author made most of his observations on cultivated and herbarium specimens.

The flowering of individual plants with phases of exclusively ♂ or ♀ flowers reduces the possibility of self-pollination (geitonogamy). However cross-pollination requires a rather synchronous flowering of protandrous and protogynous individuals. This holds as long as no flowers of the other sex are produced. In contrast to protogynous flowering specimens, which terminate the ♀ phase within a rather short period, protandrous specimens often show large variations in the duration of the ♂$_{\mathrm{I}}$ phase and partly produce ♂$_{\mathrm{II}}$ flowers or exclusively ♂$_{\mathrm{I}}$ flowers. This means that besides cross-pollination between protandrous and protogynous individuals, the protandrous specimens will also pollinate one another, which may vary the ratios in the populations.

Within some taxa the proportion of protandrous individuals strongly predominates. The large inflorescences with at most 10 per cent ♀ flowers lead to a considerable waste of pollen. (*A. nipponicum*, *A. spicatum*, *A. tonkinense*). A rather high pollen/ovule ratio was noticed for the entomophilous species *A. pseudoplatanus*: 94.000/1 (Pohl, 1937). Environmental conditions sometimes strongly reduce monoecious flowering in some habitats (*A. saccharum*: Wright, 1953; *A. nipponicum*: Ogata, 1967).

A few taxa exclusively exist of basically protandrous specimens (Series *Tegmentosa*, *A. maximowiczianum*). Their small racemose inflorescences, which never develop ♂$_{\mathrm{II}}$ flowers, usually produce flowers of one sex only. In monoecious flowering trees the ♂ and ♀ flowers are mostly distributed on different branches of the trees. A partial coincidence of anthesis of ♂ and ♀ flowers easily causes self-fertilisation (herkogamy instead of dichogamy).

The occurrence of dichogamy in *Acer* does not appear to be associated with self-incompatibility. Gabriel (1967) proved this experimentally for *A. saccharum*. The present author observed a large number of fruiting specimens of various taxa in isolated locations. These observations conflict with remarks of Fryxell (1957).

Although several seedlings of self-pollinated specimens were grown, the effects of inbreeding are still not clear.

3.5.3. *Classification of Acer on the basis of the variability in sex expression*

As a result of observations of both living and herbarium specimens and of data from literature a picture of the sex expression of most species was obtained. This picture is still rather incomplete with respect to the frequency of the various modes of sex expression within the species, and consequently within their natural populations. However, the observations gave several indications of a close agreement in sex expression of related species.

The results made it possible to distinguish 5 groups of taxa based on the variability in sex expression.

1. **Duodichogamous taxa**

These taxa are predominantly duodichogamous and protandrous. The proportion of protogynous individuals is 10–20 per cent at most. The sex expression is strongly influenced by environmental conditions. Male flowering individuals may occur, but (genetically) ♂ individuals are very probably absent. The rather large inflorescences preclude the occurrence of ♀ flowering individuals.

The flowering time is relatively late. The parthenocarpic tendency is very low.

Taxa: Series *Parviflora* and *Ukurunduensia* and some species of the most southern areas of series Sinensia e.g. *A. sinense* and *A. tonkinense.*

The same mode of sex expression was noticed in the related genera *Dipteronia* (*Aceraceae*), *Allophyllus, Deinbollia, Koelreuteria, Litchi* and other genera of the *Sapindaceae* and in the studied species of *Aesculus* (*Hippocastanaceae*).

2. Heterodichogamous taxa

The individuals of these taxa are predominantly protandrous or protogynous. The proportion of the former is ⩾ 50 per cent. Male flowering specimens may reduce this percentage, but these specimens are basically protandrous and their maleness is caused by special environmental conditions.

Protogynous specimens of some taxa occasionally produce a small number of ♂$_{I}$ flowers.

Male individuals may occur in a very low frequency, ♀ individuals are absent.

This condition is the most common in *Acer* and is present in the following taxa: Sections *Ginnala, Integrifolia, Palmata* and *Platanoidea*; series *Acer, Distyla, Macrophylla* and *Saccharodendron.*

3. Incompletely monoecious taxa

The taxa of this group are mainly composed of genetically ♂ and ♀ and protogynous individuals.

Protandrous specimens occur in a low frequency or are lacking. Female and protogynous specimens may be present in various frequencies, but together do not amount more than 50 per cent of the populations.

The inflorescences are rather small and under certain environmental conditions monoecious specimens may produce exclusively ♂ or ♀ flowers.

Taxa: Sections *Hyptiocarpa, Rubra* and *Trifoliata* (?) (excl. *A. maximowiczianum*); Series *Glabra, Monspessulana* and *Wardiana* (?).

4. Pseudo-dioecious taxa

This specialisation in *Acer* has led to taxa with basically protandrous specimens only, which are also unable to produce ♂$_{II}$ flowers. The small racemose inflorescences predominantly have ♂ or ♀ flowers and are usually not found on the same specimens. In the case of monoecious sex expression the ♂ and ♀ flowers are mostly present on separate branches.

The genetic constitution of the individuals seems to promote the production of flowers of one sex only, but environmental conditions strongly influence the ultimate sex expression and may cause large annual variations.

Taxa: Series *Tegmentosa*; *A. maximowiczianum.*

5. Dioecious taxa

The individuals are genetically ♂ or ♀. The ♀ flowers mostly lack stamens. The inflorescences predominantly develop from lateral buds only. All taxa show a strong parthenocarpic tendency.

Taxa: Sections *Negundo* and *Indivisa*; Series *Arguta* and *Lithocarpa.*

3.5.4. *Sex expression versus sex differentiation*

With a few exceptions flowers in *Acer* are functional ♂ or ♀. Bisexual flowers were noticed on single specimens of *A. macrophyllum*, *A. pensylvanicum* and *A. rubrum*. They were reported earlier for *A. rubrum* (Haas, 1933) and *A. saccharum* (Gabriel, 1960). Pollen shed of these flowers mostly occurred very late during anthesis. This strong protogyny may have led to male sterility, i.c. ♀ flowers.

Asexual flowers were observed on *A. campestre* and *A. saccharinum*. They were first described by Wahlenberg (1820) for *A. platanoides* and by Weiser (1973) for *A. pseudoplatanus*. These flowers were exclusively noticed on the borderline between ♀ and ♂$_{\mathrm{II}}$ phases. The development of their sexual organs or of the whole bud ended a few days before flowering.

The observations on a high number of living specimens during several years clearly showed the influence of environmental conditions on the sex expression in monoecious taxa. However only few data on the moment of sex differentiation of the flower buds could be collected. These data mainly concerned the borderline between the ♀ and ♂$_{II}$ phases. The occurrence of ♂$_{I}$ and ♂$_{II}$ flowers with different final stages of pistil development suggested a sex differentiation at various times before anthesis. This gap could only be filled by observations on the flower buds before anthesis (see chapter 4) and a study of the physiology of the sex differentiation (see chapter 5).

4. FLORAL INITIATION AND PREFLORAL DEVELOPMENT

4.1. INTRODUCTION

The observations of flowering led to the hypotheses that the flower buds of monoecious specimens initially were ☿ and that they differentiated at various times before anthesis into ♀ or ♂ flower buds. The latter showed pistils of various size and stage of development at anthesis ($♂_{I}$ and $♂_{II}$ flowers: see 2.4.1).

The ♂ flowers of dioecious species also have rudimentary pistils and a potential ☿ stage of the young flower bud was supposed. To establish the point of time of sex differentiation the development between flower initiation and anthesis was studied on a limited number of specimens of various species from the Wageningen Botanic Gardens, the Zuiderpark and the Gimborn Arboretum. After removal of the bud scales the floral buds were observed under a dissecting microscope.

The process of sex differentiation in *Acer* was studied by HAAS (1933) on *A. platanoides* (see 4.6). A few data in the literature were available about the time of floral initiation (4.2), the initiation of floral organs (4.3) and meiosis (4.5).

4.2. INITIATION OF INFLORESCENCES

The transition from a vegetative to a floral stage was studied by ANDERSON (1964, GUARD and ANDERSON, 1964) on *A. pseudoplatanus*. It was characterized by a gradual increase in diameter of the apex followed by a more marked increase in height. The floral apex assumed a different zonation, which consisted of a cover of meristematic cells that gave rise to the flower primordia.

HAAS (1933) observed that the floral initiation in *A. saccharinum* started about mid June and in *A. platanoides* and *A. pseudoplatanus* at about the end of June. The initiation in *A. tataricum* did not occur before 'late summer'.

The present author studied floral development in 1969 and 1970. The first initiations were observed about mid June in *A. macrophyllum* and *A. saccharinum*; at the end of June in *A. opalus*, *A. platanoides* and *A. pseudoplatanus*; at the beginning of July in *A. campestre*, *A. grosseri*, *A. negundo* and *A. rubrum*; at the end of July in *A. carpinifolium*, *A. cissifolium* and *A. henryi*; at the beginning of September in *A. ginnala*, *A. maximowiczianum*, *A. spicatum* and *A. tataricum*.

Between specimens of the same species differences of 2–3 weeks occurred in the start of floral initiation. This may be illustrated with the following observations: *A. pseudoplatanus* cv. 'Variegatum' (no. 12118) started about 3 weeks earlier than 'Prinz Handjery' (no. 11356). The same difference was noticed between *A. rubrum* 'Schesingeri' (no. 11471) and 'Sanguineum' (no. 7809). *A. campestre* 'Elsrijk' (no. 17863) was about two weeks later than 'Nanum' (no. 1766) and 'Zorgvlied' (no. 17864).

As the inflorescences of ♂ individuals of dioecious species bore more flowers than those of ♀ individuals a possible earlier start of floral initiation on ♂ individuals was supposed. However this could not be established with certainty with several specimens of *A. carpinifolium* and *A. cissifolium* growing in the 3 gardens cited above. Such a difference was also absent in protandrous and protogynous specimens of *A. pseudoplatanus* at the Wag. B.G.

Within each specimen variations in time of floral initiation occurred, mainly due to the presence of fertile long shoots of the current year. In *A. platanoides* 'Faassen's Black' (no. 13163) and 'Schwedleri' (no. 12255) floral initiation on such shoots continued until mid August. On *A. pseudoplatanus* 'Prinz 'Handjery (no. 11356) inflorescences on long shoots were initiated till the end of September, the whole initiation period on that specimen lasting about 2.5 months.

4.3. INITIATION OF FLOWER BUDS

The flower bud primordia of small racemose inflorescences, e.g. *A. grosseri*, *A. maximowiczianum* and *A. rubrum*, appeared nearly simultaneously. On the contrary, the flower bud primordia of large inflorescences were initiated successively by continuous branching of the floral axes. In the cases of *A. macrophyllum* and *A. pseudoplatanus* the terminal flower of the long rachis was initiated several weeks after appearance of the first flower bud primordia. BUCHENAU (1861) reported that on specimens of the latter species the apex of the rachis was not yet terminated by a flower bud in September. This observation could not be confirmed by the present author. In the case of species with rather large inflorescences of type I and II (see 2.3.2), the initiation period of flower bud primordia was about 6–10 weeks depending on the number of ramifications of the floral axes.

In all specimens of the studied species flower bud initiation was completed before the winter.

4.4. INITIATION OF FLORAL ORGANS

The sepal primordia appeared some days before the primordia of petals and stamens. PAYER (1857) pictured a flower bud of *A. tataricum*, which shows petal primordia and no stamen primordia. On the contrary HAAS (1933) observed in *A. pensylvanicum* an earlier appearance of the stamen primordia than of the petal primordia. The present author noticed that the petal primordia remained very small and were very soon passed by the 5 antisepalous stamen primordia.

Two other figures of PAYER's planche 27 represent the initiation of the androecium in *A. tataricum* flower buds. The 5 antisepalous primordia appeared first. They were partly, but not exactly antisepalous leaving space for the 3 antipetalous stamens, which had filled up these spaces in the next figure.

BUCHENAU (1861) and HAAS (1933), studying *A. pseudoplatanus* and *A. pensylvanicum* respectively, observed a simultaneous initiation of all stamen primordia.

The present author usually observed a rather irregularly initiation of the stamen primordia. They rarely appeared simultaneously. The antipetalous stamens mostly became visible later and lagged behind in their development, but within each whorl usually variations in appearance and development occurred.

As pointed out in 2.2.4 the stamens showed at first an obdiplostemonous arrangement.

Carpel primordia became visible after the stamen primordia had already reached a certain size. HAAS (1933) however, reported about the relatively early appearance of carpel primordia in *A. platanoides*. A relatively early appearance of the carpel primordia was only observed on flower buds of ♀ specimens of *A. carpinifolium* (no. 15723). This observation was conflicting with those on ♂ specimens of *A. carpinifolium* (no. 1773) and *A. cissifolium* (no. 1763), which did not show carpel primordia before the anthers of young stamens could be distinguished.

HAAS (1933) reported that on *A. platanoides* specimens all floral parts were present at te beginning of September and two weeks later also on specimens of *A. pseudoplatanus*. In the case of *A. tataricum* he observed no further development before the winter than the initiation of the flower primordia.

With the exception of 4 late flowering species, *A. ginnala*, *A. micranthum*, *A. spicatum* and *A. tataricum* and the lateral inflorescences on long shoots of the current year of *A. pseudoplatanus* 'Prinz Handjery' (no. 11356) the author found that all floral organs had been initiated before the winter.

4.5. MORPHOGENESIS OF THE STAMENS

The development of the stamens was not a subject of special study because in monoecious species no quantitive and qualitative differences could be observed between the anthers of ultimately functional ♂ and ♀ flowers until shortly before anthesis.

The stamens in flower buds of ♀ specimens of *A. carpinifolium*, the only dioecious species of which the androecium of ♀ flowers is not completely reduced, developed very slowly and irregularly. The anthers never contained pollen.

TAYLOR (1920) studied the meiosis in a number of species. In specimens of *A. saccharinum* meiosis took place during the second half of October. It was accompanied by a rapid increase in size of the anthers. The pollen matured before the winter. In *A. rubrum* meiosis occurred during the swelling of the buds reaching the tetrade stage as the anthers appeared between the scales at the tip. Observations on *A. negundo* agreed with those on *A. rubrum*. Despite the rather condensed inflorescences of the above mentioned species the stages were not simultaneous. Even between the locules of single anthers differences were noticed. The reduction divisions in *A. pseudoplatanus* inflorescences started largely while the inflorescences were from 10 to 15 mm in length. This size is reached just before bursting of the mixed buds and, depending on the weather conditions, from 2–3 weeks before anthesis. TAYLOR did not give any information about the ultimate sex expression of the flowers of the specimens studied.

This information was also omitted by ANDERSON (1964). She reported that with *A. pseudoplatanus* meiosis occurred aproximately mid April while flowering started in May.

4.6. MORPHOGENESIS OF OVARIES

PAYER (1857) and BUCHENAU (1861) described and pictured in great detail the development of the ovaries of *A. tataricum* and *A. pseudoplatanus* respectively. More recent data on carpel development in *Acer* are not available.

Especially during the first months after initiation the morphogenesis could be very well observed in specimens of *A. cappadocicum*, *A. macrophyllum*, *A. platanoides* and *A. pseudoplatanus*. On one inflorescence various stages of development were simultaneously present. Soon after initiation the margins of young carpels lie in nearly the same plane. The cavity of the carpels becomes larger and is gradually filled by the two ovules. Seen from above these ovules look like a four-leaved clover Gradually the angle between the margins of the carpels decreases, while their margins become connate from the basis. When carpels are completely connate their tips elongate, forming a style or two stigmas. At about the same time the differentiation of the wings starts.

An ovary reaching this stage of development could be found in ♀ or $♂_{II}$ flowers, and in $♂_{I}$ flowers of series *Tegmentosa*. Morphologically the differences between the ovaries of these flowers are quantitative. Pistil development ceases rather abruptly in $♂_{II}$ flowers shortly before flowering.

As pointed out in 2.2.1 ♂ flowers of dioecious species usually have a rudimentary pistil. It was observed that the initiation of these pistils was relatively late during the development of the flower bud (see 4.4). The two carpels remained disconnate and did not contain ovules. Sometimes they elongated to scrufulous hairs. Occasionally the ovary consisted of a single carpel. In *A. carpinifolium* (no. 1773) and *A. cissifolium* (no. 1763) it was observed that the carpel primordia showed no further development. At anthesis these primordia were invisible. They were probably overgrown by the honey disc.

In the ♂ *A. rubrum* cv. 'Schlesingeri' (no. 11472) the development of the ovaries was retarded after mid August. At that time the margins of the carpels made an angle of about 120°. The ovules became somewhat bulged above these carpel margins. The development of the carpels slowly continued. Finally their margins extended above the ovules, but the ovary often did not reach the closed stage and usually no stigmas developed. Another ♂ cv., 'Taranto' (no. 15724), which had a later start of floral initiation, did not show irregularities before mid September. However, variations in the stage of development were also present between ♀ cv.'s. The carpels of 'Tilford' (no. 14861) were completely connate at the beginning of September, while in 'Sanguineum' this stage was not reached before the beginning of October.

In *A. macrophyllum* (no. 1779) and *A. pseudoplatanus* 'Variegatum' (no. 12118) the first irregularities in pistil development of ultimately ♂$_{\mathrm{I}}$ flowers became visible at the end of January. The (closed) ovaries of the oldest flower buds looked somewhat paler than those of younger buds. Comparison of the ovaries of 'Variegatum' with those of protogynous flowering specimens such as 'Costorphinense' (no. 8382) and 'Leopoldii' (no. 11460) did not show any morphological (and quantitative) difference except the somewhat pale-green colour. The measurement of ovaries showed large variations between the specimens but no clear correlation with the ultimate sex of the flowers.

Despite the absence of a protogynous specimen interesting observations could be made on *A. macrophyllum*. During February the ovaries became hairy. Those of ultimate ♀ and ♂$_{\mathrm{II}}$ flowers became completely hairy, those of the ultimate ♂$_{\mathrm{I}}$ flowers became only partly so. Especially the oldest flower buds show hairs on the base of the ovaries only. The last flowers of the ♂$_{\mathrm{I}}$ phase had more hairs, but they lacked hairs on the upper part of the carpels and on the wings. Although during February the ultimate ♂$_{\mathrm{I}}$ phase could be recognized, the ovaries of the ♂$_{\mathrm{I}}$ flower buds still showed some growth and developed small wings and stigmas (see fig. 30).

The ovaries of *A. pseudoplatanus* flower buds became hairy during April. No variations could be observed during this process between ultimate ♂$_{\mathrm{I}}$ and ♀ flowers, while further observations were impossible because of the strong hairiness.

It was further found that the carpels of *A. maximowiczianum* (no. 794) were not yet completely connate one month before flowering.

HAAS (1933) compared pistil development between terminal flowers of a protandrous and a protogynous *A. platanoides* specimen by daily observation from the end of March. The first variations were noticed about three weeks before anthesis.

4.7. DISCUSSION AND CONCLUSIONS

Initiation of inflorescences started about 8–9 months before flowering, variations in this start between specimens of a species partly corresponding with small variations in the onset of anthesis.

Results of 5 years of observation in apple, pear and cherry cultivars by ZELLER (1955) showed a strong correlation between the flowering time and the subsequent floral initiation. This relationship was not studied in *Acer*.

The view that protandrous specimens of monoecious and ♂ specimens of dioecious species started the initiation of inflorescences earlier than protogynous and ♀ specimens could not be confirmed. For such a study the number of available specimens was too limited; besides, such a study should preferently be made in the natural habitats of the species. Flower bud initiation took much more time than anthesis. Especially on long shoots of the present year this initiation could be delayed for several weeks. This is in agreement with observations on apple and pear cultivars, which also flower on one-year-old long shoots (Zeller, 1960; Staritsky, 1970).

The sequence of anthesis of flowers within inflorescences corresponded with the developmental sequence, e.g. the terminal flowers on the rachis of *A. pseudoplatanus* inflorescences (see 3.3 series *Acer* par. 9).

Observations by several authors (e.g. Zeller, 1955; Brown and Kotob, 1957; Staritsky, 1970) showed that the development of the flower buds of various fruit trees continues during the winter months in temperate climates. Late flowering cultivars of apricot and apple had a deeper dormancy than early flowering cultivars and hardly show any development during the winter (Brown, 1957; Zeller, 1955). A continuous development of flower buds was also noted on the *Acer* species studied.

Flower buds of ♂ and ♀ *A. carpinifolium* specimens show a different bisexual stage during their development. Ovary primordia appeared relatively late in ♂ flowers, while in ♀ flower buds stamens were initiated nearly simultaneously with the carpels. In *A. rubrum* on the contrary differences between ovaries in flower buds of ♂ and ♀ specimens could be observed only at the end of August, about two months after the initiation of the inflorescences, all flower buds having a similar bisexual development for at least two months after initiation. The development of the stamens of ♂ and ♀ flowers in this and other monoecious species showed no difference until very shortly before anthesis.

It was not possible to establish the moment of sex differentiation on the remaining monoecious species studied by observations of the ovary development. After the differentiation into ♂$_{\mathrm{I}}$ flower buds there was no complete cessation of the ovary development. Measurements of ovary diameters showed large variations within single inflorescences and also between the ovaries of flower buds with corresponding positions in inflorescences of specimens of the same species. *A. macrophyllum* showed that the ovaries of ultimately ♂$_{\mathrm{I}}$ flowers obtained a pale green colour during February and became less hairy than the remaining ovaries. The light-green colouring of aborted ovaries was also observed on protandrous specimens of *A. pseudoplatanus*.

The occurrence and duration of the ♂$_{\mathrm{I}}$ phase of protandrous specimens depends on a number of internal and external factors. The stage of development reached by the flower buds during late winter and early spring, when differentiation into ♂$_{\mathrm{I}}$ flower buds occurs, will show yearly variations, variations between specimens of the same species and between the inflorescences of single specimens. This may be due to the time of initiation of the inflorescences in relation to the previous flowering period, the competition of fruits (see 5.3), the health status, and the location of the trees, and the weather conditions throughout flower development.

The process of sex differentiation was further studied in some physiological experiments dealt with in the next chapter. Part of the experiments gave information on the differentiation of ♀ and ♂$_{\mathrm{II}}$ flowers. For a general discussion on sex differentiation see 5.7.

5. THE PHYSIOLOGY OF SEX DIFFERENTIATION

5.1. General introduction

The observations on the variability of the sex expression in *Acer* described in Chapter 3 clearly showed the role of genetic and environmental factors. The results arouse interest to study the mechanism of these sexual changes.

Observations of Haas (1933) on *A. platanoides* (see 4.6) indicated that the sex differentiation of ♂$_{I}$ flowers took place only a few weeks before anthesis. The first experiments were based on this information and also aimed at studying the possible role of phytohormones in sex differentiation. The experiments, in which detached branches were mainly used, gave rise to further study of sex differentiation of ♂$_{I}$ flowers by forcing detached branches into flower (see 5.2).

Some experiments were made to determine the influence of leaves on the sex differentiation. The results also support information on the differentiation of ♂$_{I}$ flowers (see 5.3).

The observed influence of ♀ buds and ♀ flowers on the differentiation of ♂$_{II}$ flowers was studied by removal of ♀ flower buds at intervals before anthesis (see 5.4).

The functional male sterility of ♀ flowers was studied with the aid of sterile culture of ♀ flowers and undifferentiated flower buds (see 5.5).

Finally results are given of germination tests of pollen from the various types of flowers (see 5.6).

5.2. The influence of accelerated flowering on sex expression

5.2.1. *Introduction and literature*

Studying the role of phytohormones on the sex expression with detached branches, which were forced into flower during early spring, an effect was found that only could be attributed to accelerated flowering. This led to further experiments which were specially made to obtain information on the time of sex differentiation of the ♂$_{I}$ flowers.

Heslop-Harrison (1957, 1972) and Napp-Zinn (1967) reviewed the literature on the regulation of sex expression in higher plants. Their data on accelerated flowering mainly concern the effects induced by continuous short-day treatment resulting in a lower ♂/♀ ratio in several short-day plants. These experiments give no link with the present study, in which accelerated flowering was used as an aid in following the development of the flower buds outdoors, i.e. their differentiation to ♂$_{I}$ flowers during winter and early spring.

5.2.2. *Materials and methods*

Branches of 40–60 cm length with sufficient mixed buds were cut from a number of specimens in the Wag. B.G., representing 11 species of 7 sections in all. The branches were taken from the periphery of the crown, preferably branches without a strong ramification. Sometimes the branches were stored for different periods of time in a refrigerator at 1–3 °C or were partly buried in the soil outdoors.

The lower most 30 cm of the branches was placed in a 0.02% solution of 'Venturicide' (Verdugt, The Hague; contains 2.5% phenyl-mercurychloride) for 4–6 hours. A small piece of the base was then cut off under water and the branches were placed in vessels. Initially a medium developed by SYTSEMA (1962) for lilac branches was used. Better development of the branches was obtained after application of 'Chrysal' and 'Heersterchrysal' (Fa. Bendien, Naarden, The Netherlands). The first product improves the keeping quality of cut flowers. The latter was specially developed as a pretreatment of branches of woody ornamentals and contains sugars, bactericide, fungicide and ingredients, which suppress polyphenol oxydase activities.

Three to four branches per vessel containing distilled water with 15 g/l 'Heesterchrysal' were placed in a room with a low relative humidity and a constant temperature of 25 °C for two days. This treatment with 'Heesterchrysal' was omitted when the branches already showed swelling buds, in which stage this treatment caused harmful side-effects. The branches were next transferred to vessels containing 15 g/l 'Chrysal' (contains sugars, fungicide, bactericide). In some experiments 10^{-4}, 10^{-5} or 10^{-6} M GA_3 (gibberellic acid) or NAA (1-naphthyl acetic acid) were added. The vessels were placed in climate chambers at a minimum relative humidity of 80%, 20 °C during 12 hrs illumination (fluorescent and incandescent lamps; red light 0.072, blue light 0.085 Watt m^{-2} nm^{-1}) and 5 °C at night. In some experiments other temperatures were used.

The medium was supplemented with 'Chrysal' solution of the same concentration. After 2–3 weeks the medium was renewed without repetition of the hormonal treatment. Sediments of the branches were removed.

5.2.3. *Results*

The experiments will be reported per section per species.

Section Acer

Acer pseudoplatanus

The first experiments were made with one-year-old long shoots of 'Variegatum' (no. 12118). The branches developed several large terminal and lateral inflorescences which often led to early exhausting and withering of the branches. Better results were obtained with no. 7191, which was exclusively used in the second year. Table 15 presents the results for both specimens. The inflorescences of 'Variegatum' are distinguished according to their position on the shoots. The terminals were much larger and showed a relatively shorter $♂_{I}$ phase (% of all flowers), which was most pronounced in the experiments started in February and March.

The results of GA_3 treatment are only shown for the first experiment, because

TABLE 15. Sex expression of detached branches of two protandrous *Acer pseudoplatanus* specimens forced into flower at various times before flowering outdoors.

specimen; of Wag. B.G. starting date of experiment	terminal (T) or lateral (L) posed inflor.	temperature day/night	GA_3 conc. in mol.	starting date of flowering	number of florescences	mean number of flowers per inflorescence			
						♂$_{\mathrm{I}}$	♀	♂$_{\mathrm{II}}$	total
'Variegatum' (no. 12118)									
12/2/70	T + L	20/20+20/5	10^{-5}		13	1	18	36	55
12/2/70	T + L	20/20+20/5	–		13	3	18	26	57
12/2/70	T	20/20+20/5	–		17	1	20	43	64
12/2/70	L	20/20+20/5	–		9	5	13	23	42
5/3/70	T	20/ 5	–		12	18	21	31	69
5/3/70	L	20/ 5	–		8	13	9	16	38
5/3/70	T + L	20/ 5	–		20	16	16	25	57
9/4/70	T	20/ 5	–		16	48	25	30	103
9/4/70	L	20/ 5	–		39	30	10	13	53
9/4/70	T + L	20/ 5	–		55	35	15	19	68
1/5/70	T	20/ 5	–		10	72	26	17	115
1/5/70	T	20/ 5	–		15	42	11	3	56
1/5/70	T + L	20/ 5	–		25	54	17	9	79
outdoors	T			9/5/70	10	72	36	21	129
outdoors	L			9/5/70	16	41	7	0	49
outdoors	T + L				26	53	18	9	79
no. 7191									
18/3/70		20/ 5	–	4/4/70	19	23	15	23	61
9/4/70		20/ 5	–	20/4/70	41	32	15	17	63
1/5/70		20/ 5	–	10/5/70	19	48	15	6	69
outdoors		20/ 5	–	9/5/70	23	44	15	5	64
14/12/70		25/15	10^{-5}	8/1/71	7	0	12 withered during ♀ phase		
14/12/70		25/15	–	12/1/71	4	2	7 withered during ♀ phase		
18/1/71		22/15	10^{-5}	6/2/71	7	2	18	21	41
18/1/71		22/15	–	8/2/71	8	6	15	13	35
17/2/71		20/10	10^{-6}	6/3/71	13	9	17	12	38
17/2/71		20/10	–	6/3/71	14	14	15	11	39
8/3/71		20/10	10^{-6}	22/3/71	7	15	not established		
8/3/71		20/10	–	22/3/71	9	16	not established		
7/4/71		22/15	–	15/4/71	12	38	9	10	57
outdoors				21/5/71	21	52	9	5	66

several inflorescences withered during anthesis and the results of the remaining inflorescences did not differ from those of untreated branches.

The ♂$_{\mathrm{I}}$ phase in both specimens increases until very shortly before the bud break, i.e. about one week before the onset of anthesis. Although flowering started later in 1970 the ♂$_{\mathrm{I}}$ phase of no. 7191 was shorter in that year than in 1971, while the average number of flowers per inflorescence did not differ.

Some experiments with the protogynous specimen no. 8385 only resulted in normal flowering as observed outdoors.

Acer opalus

Branches of the ♂ flowering no. 2689 were detached on October 26, 1970 and stored in a refrigerator at 1–3 °C. From November 20, 1970 they were forced, with 10^{-5} M GA_3 to break dormancy. Only ♂ flowers were produced. It may be concluded that this specimen is genetically ♂ and differentiation took place before November.

Section Platanoidea

Acer campestre

Three cultivars of these species were used in the experiments: 'Elsrijk' (no. 17863), protogynous; 'Zorgvlied' (no. 17864), protandrous and 'Nanum' (no. 1766), flowering ♂ during most years of observations.

The experiments with the dwarf c.v. 'Nanum' caused problems, because the strongly ramified branches with several mixed buds often showed a rather poor development and withered during anthesis.

The inflorescences frequently developed irregularly, especially the lowest secondary axes were backward. Only part of the branches of 'Nanum' produced reliable results.

All specimens showed a strong reduction of the ♀ phase. Frequently ♀ flower buds on the borderline of the ♀ and the $♂_{II}$ phase or even all ♀ buds failed to flower, or showed extension of one or two filaments during the $♂_{II}$ phase, followed by pollen shed of the anthers. This phenomenon was also observed in the field in 'Elsrijk'.

In table 16 the results are given of 'Nanum' and 'Zorgvlied'. In the first experiment of 1970 three temperature conbinations were used. The lowest day temperature (15 °C) led to a much slower development of 'Nanum' branches and also to a longer $♂_{I}$ phase. These differences were smaller in the case of 'Zorgvlied'. In the second trial with 'Nanum' in 1970 (March 5) NAA and GA_3 had no effect and therefore the results were not specified in the table.

In 1970 'Nanum' produced some ♀ flowers outdoors, while the mean number of flowers per inflorescence was higher than in 1971. These ♀ flowers were mainly found in some of the largest inflorescences, localized on specific branches.

The results of both specimens indicate that $♂_{I}$ flowers are differentiated between the end of January and a few days before the bursting of the mixed buds.

The protogynous 'Elsrijk' showed this type of flowering in all experiments including GA_3 treatments. Branches detached on March 26, 1970 and stored in a refrigerator at 1–3 °C were forced into flower at the end of June 1970. They also produced their ♀ flowers first.

Acer platanoides

The specimens used were cv. 'Faassen's Black' (no. 13163) and 'Globosum'

TABLE 16. Sex expression of detached branches of *Acer campestre* 'Nanum' and 'Zorgvlied', forced into flower at various times before flowering outdoors.

starting date of experiment	temperature day/night	GA$_3$ conc. in mol.	starting date of flowering	number of inflorescences	mean number of flowers per inflorescence			
					♂$_\mathrm{I}$	♀	♂$_\mathrm{II}$	total
'Nanum' no. 1766								
2/ 4/70	20/20		24/2/70	20	0.5	0.8	6.0	7.3
2/ 4/70	20/ 5			41	0.6	0.3	5.1	6.0
2/ 4/70	15/10			45	3.7	1.4	3.2	8.3
5/ 3/70	20/ 5		23/3/70	66	5.1	0.1	4.6	9.8
25/ 3/70	20/ 5			61	4.6	0.8	3.3	8.6
9/ 4/70	20/ 5		16/4/70	40	6.1	1.8	4.1	12.0
29/ 4/70	20/ 5			22	11.0	0.3	–	11.3
outdoors			5/5/70	58	13.4	0.2		13.7
14/12/70	25/15	10^{-5}	8/1/71	8	–	withered during ♀ phase		
14/12/70	25/15	–			withered before flowering			
18/ 1/71	22/15	10^{-5}	4/2/71	1	–	withered during ♀ phase		
18/ 1/71	22/15	–	4/2/71	26	0.1			
17/ 2/71	20/10	–	1/3/71	30	1.0			
10/ 3/71	20/10	–	19/3/71	11	4.0		5.6	9.6
7/ 4/71	22/15	–	13/4/71	9	9.0		1.3	10.3
outdoors			29/4/71	24	11.4	–	–	11.4
'Zorgvlied' no. 17864								
25/ 2/70	20/ 5			30	1.5	1.9	7.6	11.0
25/ 2/70	20/ 5			32	2.1	1.4	8.1	11.7
18/ 3/70	20/ 5			29	5.3	1.2	10.0	16.5
1/ 5/70	20/ 5			69	10.6	3.4	1.5	15.6
outdoors				75	9.8	4.7	1.2	15.7
18/ 1/71	22/15	10^{-5}	6/2/71	12	–	2.4	6.4	8.8
18/ 1/71	22/15	–	10/2/71	16	–	2.0	8.6	10.6
17/ 2/71	20/10	10^{-5}	3/3/71	21	0.6	3.2	8.1	11.9
17/ 2/71	20/10	–	6/3/71	12	0.9	3.1	8.6	12.6
8/ 3/71	20/10	10^{-5}	21/3/71	14	1.1	2.4	7.6	11.1
8/ 3/71	20/10	–	21/3/71	14	1.6	2.5	7.1	11.2
7/ 4/71	22/15	–	15/4/71	42	6.1	2.4	4.3	12.8
outdoors			30/4/71	70	8.3	3.8	1.5	13.6

(no. 11454), both protogynous, and nos. 1774 and 12116 of the protandrous cv. 'Reitenbachii'. From the 70-year-old no. 1774 some large branches were pruned by the gardeners during the autumn of 1970. In view of the scarcity of material of protandrous specimens a part of this material was put in plastic bags and stored in a refrigerator at 1–3 °C, while the remaining part was buried in the soil outdoors. It was supposed that the environmental conditions of the latter branches resembled those of the tree. In one experiment some braches were forced, which were left under the tree for 4 weeks.

The results of the experiments are shown in table 17. Stored branches differentiated no ♂$_\mathrm{I}$ phase before February, while in March the mean number of ♂$_\mathrm{I}$ flowers per inflorescence was still very low. The first experiments with fresh

TABLE 17. Sex expression of detached branches of two specimens of *Acer platanoides* 'Reichenbachii' (Wag. B.G. nos. 1774 (= A) and 12116 (= B)) forced into flower at various times before flowering outdoors.

starting date of forcing	specimen	temperature day/night	hormones conc. in mol.	starting date of flowering	number of inflorescences	mean number of flowers per inflorescence			
						♂$_{\mathrm{I}}$	♀	♂$_{\mathrm{II}}$	total
4/ 2/70	B	20/20	NAA10^{-5}		23	8	7	11	26
4/ 2/70	B	20/20	–		30	8	6	11	25
4/ 2/70	B	20/ 5	NAA10^{-5}		21	5	5	15	25
4/ 2/70	B	20/ 5	–		26	6	6	13	26
4/ 2/70	B	15/10	NAA10^{-5}		20	9	5	10	24
4/ 2/70	B	15/10	–		31	13	7	11	30
11/ 3/70	B	20/ 5	GA10^{-5}		23	13	6	13	32
11/ 3/70	B	20/ 5	–		27	12	7	11	31
11/ 3/70	B	15/10	GA10^{-5}		25	12	7	12	31
11/ 3/70	B	15/10	–		25	14	8	10	31
22/ 4/70	B	20/ 5	–		17	12	12	14	39
22/ 4/70	B	15/10	–		23	14	10	9	33
outdoors					55	12	77	6	34
20/11/70[1]	A	25/15	GA10^{-5}	9/12/70	5	– withered during ♀ phase			
20/11/70[1]	A	25/15	GA10^{-6}			withered before flowering			
14/12/70[1]	A	25/15	GA10^{-5}	30/12/70	8	– withered during ♀ phase			
14/12/70[1]	A	25/15	–	4/ 1/71	15	–	4	17	21
18/ 1/71[1]	A	22/15	GA10^{-5}	2/ 2/71	9	–	8	21	29
18/ 1/71[1]	A	22/15	GA10^{-5}	4/2/71	12	–	5	23	29
18/ 1/71[2]	A	22/15	–	2/2/71	5	–	6	20	26
17/ 2/71	A	20/10	–	1/3/71	20	4	6	10	21
17/ 2/71[1]	A	20/10	–	1/3/71	7	0.1	8	16	24
17/ 2/71	B	20/10	–	1/3/71	13	6	5	11	23
10/ 3/71	A	20/10	–	19/3/71	10	14	4	5	23
10/ 3/71[3]	A	20/10	–	19/3/71	7	4	8	14	26
10/ 3/71[1]	A	20/10	–	19/3/71	10	1	9	18	27
10/ 3/71	B	20/10	–	19/3/71	25	12	6	7	25
7/ 4/71	B	22/15	–	11/4/71	10	13	7	4	24
outdoors	A			20/4/71	45	12	13		24
outdoors	B			21/4/71	45	14	11	2	28

[1] Detached on Oct. 26, 1970 and stored at 1–3 °C; [2] Detached on Oct. 26, 1970 and stored outdoors; [3] Detached on Feb. 17, 1971 and left behind outdoors.

material were not made before February. The occurrence of a distinct ♂$_{\mathrm{I}}$ phase indicated that differentiation of ♂$_{\mathrm{I}}$ flowers on the tree started in January at the latest. The branches, which were left outdoors after detachment for 4 weeks produced the same mean number of ♂$_{\mathrm{I}}$ flowers as directly forced branches (4.3 against 4.4).

The effect of GA_3 is clearly shown in the experiments carried out from November till January. The only branches which came into flower in November were those of the highest GA_3 concentration. Branches forced in December showed an advance in onset of flowering of 5 days, those forced in January flowered 2 days earlier after GA_3 treatment.

In one experiment (1970) branches were forced with various temperatures, while part of the branches were placed in a medium to which NAA was added. NAA in combination with the day-night temperatures 20/20 and 20/5 °C resulted in a relatively shorter ♂$_{I}$ phase, anthesis also starting some days earlier. The branches forced at 15 °C at day and 10 °C at night produced twice as many ♂$_{I}$ flowers than those forced with 20 °C at day and 5 °C at night, while anthesis of the latter started one week earlier.

The branches forced from March 7, 1970 and March 3, 1971 produced about the same mean number of ♂$_{I}$ flowers as were counted on the tree in April. The differentiation of ♂$_{I}$ flowers appears to finish in the beginning of March, when the buds already show some swelling.

The protogynous cv. 'Globosum' was forced at various times and partly treated with NAA and GA_3. Only protogynous inflorescences were obtained. This also occurred with branches of Faassen's Black' stored from March 26, 1970 and brought into flower at the end of June. 'Globosum' sometimes showed asexual flowers on the borderline of the ♀ and ♂$_{II}$ phases. They could hardly be distinguished because they looked like flower buds, which would open within one or two days. These flowers were not observed on the tree.

Section Palmata

Acer circinatum

From the small shrub no. 17525 only few branches could be taken. Table 18 shows a decrease of the ♂$_{I}$ phase after the degree of accelerated flowering.

The temperature effects correspond with those found for *A. platanoides* 'Reitenbachii' and *A. campestre* 'Nanum'.

As pointed out in 3.3. III *Palmata* par. 7 protandrous specimens of *A. circinatum* mostly produce 2 ♀ flowers per inflorescence against protogynous specimens only one. When accelerated flowering led to protogyny, then the inflorescences also produced a single ♀ flower.

TABLE 18. Sex expression of detached branches of *Acer circinatum* (Wag. B.G. no. 17525) forced into flower at various times before flowering outdoors in 1970.

starting date of experiment	temperature day/night	starting date of flowering	number of inflorescences	mean number of flowers per inflorescence			
				♂$_{I}$	♀	♂$_{II}$	total
2/4	20/ 5	7/3	14	1.1	1.1	6.1	8.4
2/4	15/10	16/3	20	2.2	1.6	2.4	6.2
18/3	20/ 5	4/4	11	2.2	1.1	0.8	4.1
18/3	15/10	4/4	16	2.8	1.4	1.4	5.7
29/4	20/ 5	2/5	19	3.7	0.6	0.6	4.8
outdoors		4/5	30	3.8	1.7	1.6	7.1

Acer palmatum

During observations at Boskoop two male flowering specimens were found 'Decompositum' and a specimen provisionally indicate there as ('Palmatum'). Material of these specimens partly treated with 10^{-5} and 10^{-6} M GA_3 was forced from February 2, 1971. The branches showed a moderate development. Those inflorescences which flowered completely only produced $♂_{I}$ flowers. Very probably these specimens are genetically male.

Section Macrantha

Acer grosseri

The only specimens of section *Macrantha*, which regularly produced ♂ flowers were *A. grosseri* no. 13167-I and no. 17788.

However they were rather small and could supply few experimental material. Branches were forced during the winter of 1970-71. All experiments started between December 16, 1970 and March 18, 1971 resulted in complete ♀ flowering, while branches forced from April 7, 1971 flowered completely ♂. The latter experiment started one week before anthesis of the trees.

Although outdoors both specimens produced besides ♂ inflorescences some ♀ and androgynous inflorescences, these inflorescences were localized on some poorly developed branches (no. 13167-I) or on one main branch from which no material was taken (no. 17788).

In the December and January experiments 10^{-5} M GA_3 shortened the number of days before anthesis.

Branches of the predominantly ♀ flowering no. 12997 produced exclusively ♀ flowers after forcing at various times and after treatment with 10^{-5} M GA_3.

Acer rufinerve

Branches detached on March 26, 1971 were stored in a refrigerator and brought into flower at the end of June. They flowered completely ♀ as did the shrub during the spring of 1971 too.

Section Trifoliata

Acer maximowiczianum

This species has some properties which made it very suitable for experiments. The inflorescences predominantly had only 3 flowers, while $♂_{II}$ flowers were never observed. An androgynous inflorescence usually has a $♂_{I}$ terminal flower and a ♀ flower on the two side axes. Monoecious flowering trees usually showed branches with various ♂/♀ ratios.

A large specimen in Wag. B.G., no. 794, exclusively produced ♂ flowers between 1966 and 1975, except in 1969 and 1970, when a few ♀ flowers were found in a small part of the crown.

From March 18, 1969 branches were forced into flower in Sytsema's medium to which 0.5×10^{-4}, $0{,}5 \times 10^{-5}$ and 0.5×10^{-6} M NAA was added. The branches treated with NAA developed well and produced some ♀ flowers within 4 weeks. At first this ♀ sex expression was attributed to NAA but some days

TABLE 19. Sex expression of detached branches of *Acer maximowiczianum* (no. 794) forced into flower at various times before flowering outdoors in 1970.

starting date of experiment	starting date of flowering	number of inflorescences	sex expression of the inflorescences (%)		
			♂	♂-♀	♀
5/3	15/4	47			100
2/4	25/4	45			100
9/4	30/4	81			100
20/4	8/5	132	14	38	48
29/4	16/5	94	48	38	13
6/5	21/5	103	79	16	6
outdoors	19/5	∞	100	< 0.1	< 0.1

later the untreated branches also produced ♀ flowers exclusively. In a second experiment, which started on April 18, 1969, GA_3, IAA and NAA were used in the above mentioned concentrations. The branches developed ♂, ♀ and androgynous inflorescences (flowering types E, B and D respectively) independently of the hormonal treatment. Androgynous inflorescences mostly had a ♂ terminal flower, while the two side axes had a ♀ flower.

In 1970 branches were forced from the beginning of March. As shown in table 19 the first experiments led to completely ♀ flowering. Addition of GA_3 or NAA (conc. 10^{-5} and 10^{-6} mol.) resulted in a quicker development of the branches, while the first flowers opened 10, 3 and 2 days earlier than those of the untreated branches. Data on the latter are given in the table.

The first ♂ flowers appeared in the experiment started on April 20, 1970. Their proportion strongly increased in the two following experiments. From these results it may be concluded that sex differentiation on the tree started within 6 weeks of flowering and continued till less than 2 weeks before anthesis.

The branches of the latest experiment started anthesis 2 days later than the tree outdoors. The occurrence of ♀ flowers on these branches strongly contrasts with the predominantly ♂ flowering tree. The cause of this variation is not clear. There were rather small differences between temperatures outdoors and in the experiment. The mean night temperature outdoors was somewhat higher. The rainfall in this period was very low (4 mm). The vegetative development of the branches show less progress in the experiment than outdoors. This may lead to a stronger competition with the flower buds outdoors.

Section Rubra

Acer rubrum

Branches of one ♀ specimen, 'Sanguineum' (no. 7809) and 3 ♂ specimens, 'Schlesingeri' (no. 11472), 'Taranto' (no. 15724) and one from the Gimborn Arboretum were forced into flower from October 26, 1970. Only those branches with 10^{-5} M GA_3 in the medium reached the flowering stage. 'Taranto', which has a relatively late flower induction, was the only specimen showing deviation from the normal sex expression. In the first experiment (October 26,

TABLE 20. Sex expression of detached branches of *Acer macrophyllum* (Wag. B.G.) no. 1779) forced into flower at various times before flowering outdoors.

starting date of experiment	temperature day/night	GA_3 conc. in mol.	starting date of flowering	number of inflorescences	mean number of flowers per inflorescence			
					♂$_I$	♀	♂$_{II}$	total
20/11/70	25/15	10^{-5}	12/8/70	1	–	withered during ♀ phase		
17/12/70	25/15	10^{-5}	8/1/70	5	–	14	withered after ♀ phase	
17/12/70	25/15	–	withered before flowering					
18/ 1/71	22/15	10^{-5}	2/2/71	10	3	11	withered after ♀ phase	
18/ 1/71	22/15	–	9/2/71	very irregularly, precocious bud drop				
17/ 2/71	20/10	10^{-6}	24/2/71	4	30	11	8.0	49
17/ 2/71	20/10	–	24/2/71	5	31	13	4.0	48
26/ 2/71	22/15	–	5/3/71	11	33	11	7.0	51
outdoors			18/4/71	14	35	22		57

1970) the flowers were functionless (= asexual). However, their pedicels elongated during anthesis in the same way as those of ♀ flowers of this species. This penomenon was not found in subsequent experiments indicating that the ultimate differentiation into ♂$_I$ flowers occurred at the end of October in this specimen.

Section Lithocarpa

Acer macrophyllum

This early flowering species with large inflorescences appeared to be a rather difficult one to force properly. The experiments in the spring of 1970 yielded poor results. A large number of flower buds failed to flower.

Because of the interesting observations on ovary development (see 4.6) branches of no. 1779 were again forced from November 1970. As shown in table 20 the first experiment only succeeded when the medium contained GA_3. Initially all branches developed fairly well, but after 3–4 weeks they withered within a few days. The results show a strong increase in the percentage of ♂$_I$ flowers after their first appearance in the experiment started on January 18, 1971. Within about one month the differentiation of the whole ♂$_I$ phase seems to be realised. This period ends 6–8 weeks before anthesis.

In the first decade of March most of the swelling mixed buds were frosted during some very cold nights (minimum temperatures of 12–18 °C below zero) after the rather mild weather of February. Only few inflorescences were available to establish the mean number of ♂$_I$ flowers on the tree.

5.3. INFLUENCE OF DEFOLIATION ON SEX EXPRESSION

5.3.1. *Introduction and literature*

In some experiments specimens of a number of species were defoliated at various times before anthesis to determine a possible regulating effect on the sex expression. Such effects were reported by GALUN (1959) for cucumber (*Cucumis sativus* L.). Removal of young leaves promoted the production of ♂ flowers, removal of old leaves that of ♀ flowers. He concludes that auxin production of young leaves furthered the development of ♀ flowers.

A. W. DE JONG and BRUINSMA (1974a) found that removal of adult leaves of *Cleome spinosa* L. plants increased pistil abortion in the bisexual flowerbuds, whereas removal of young leaves had no effect on pistil development.

5.3.2. *Defoliation after flower induction*

On August 2, 1970, during or just before the initiation of flower buds, with specimens of several species part of the branches were completely defoliated: *A. campestre* 'Nanum' (no. 1766); *A. carpinifolium* (no. 1773), ♂; *A. grosseri* (no. 12997); *A. negundo* var. *californicum* (no. 13166), ♂; *A. platanoides* (s.n.), protandrous; ibid. 'Reitenbachii' (no. 12118), protandrous; *A. rubrum* 'Schlesingeri' (no. 11472), ♂; ibid. 'Tilford' (no. 14861), ♀; ibid. no. 1757-II, ♂/♀; *A. rufinerve* (no. 12471). From the only fruit bearing specimen 'Reitenbachii', the fruits of some defoliated branches were also removed. In the case of *A. rubrum* the vegetative buds on some of the treated branches were removed.

All treated specimens showed a slower development during budding and a 1–7 days later onset of flowering. The sex expression did not differ from that of the untreated part of the trees except in *A. platanoides* (see table 21). Defoliation led to a slight reduction in the number of flowers per inflorescence and in the number of ♂$_{\mathrm{I}}$ and ♀ flowers. The treated branches of both specimens lagged behind in development, while the changes of the ♂ and ♀ phases occurred somewhat later. This delay was most clear on the defoliated branches of 'Reitenbachii', which were 4 days behind. The ♂$_{\mathrm{I}}$ phase was distinctly shorter, while a few inflorescences flowered protogynously. This effect is mainly due to the presence

TABLE 21. Sex expression of two protandrous *Acer platanoides* specimens after partly defoliation during the preceding summer.

specimen treatment	starting date of flowering	number of inflorescences	mean number of flowers per inflorescence			
			♂$_{\mathrm{I}}$	♀	♂$_{\mathrm{II}}$	total
Wag. B.G. s.n. defoliated (Aug. 2, 1970)	20/4/71	19	8	7	2	18
control	19/4/71	26	9	9	2	20
'Reitenbachii' Wag. B.G. no. 12116						
defoliated (Aug. 2, 1970)	26/4/71	52	8	11	8	26
ibid., fruits removed	23/4/71	129	12	12	4	29
control	22/4/71	45	14	15	3	31

of the fruits on the branches which apparently delays flowal development. When the fruits were also removed the delay was restricted to one day only. *A. rubrum* (no. 1757) flowered predominantly ♂, while the defoliated branches exclusively produced ♂ flowers. On cv. 'Tilford' the removal of vegetative buds led to a parthenocarpic development of the fruits (see 2.5.2).

5.3.3. *Defoliation during unfolding of the leaves*

During the unfolding of the leaves some branches of the protandrous flowering specimens *A. ginnala* no. 8330 and *A. pseudoplatanus* no. 17717 were defoliated. The treatment had no influence on the development of the inflorescences and the duration of the ♂$_{\mathrm{I}}$ phase. A possible influence on the ♀ phase was not investigated.

5.4. INFLUENCE OF FLOWER BUD REMOVAL ON SEX EXPRESSION

5.4.1. *Introduction and literature*

In a number of small experiments flower buds were removed at various times after the bursting of the mixed buds. This mainly concerned buds which should develop into ♀ flowers. These experiments were made to obtain more information about the moment of differentiation of ♂$_{\mathrm{II}}$ flowers and the possible influence of ♀ flower buds on this differentiation.

Several authors described the influence of inflorescence mutilations on the sex expression of the remaining flower buds. Murneek (1927) found that removal of young fruits or pistils of ♀ flowers of *Cleome spinosa* L., decreased the ♂/☿ ratio. A.W. de Jong and Bruinsma (1974b) made an extensive study of the physiological background of this phenomenon in *Cleome*, an andromonoecious flowering plant with alternate phases of ☿ and ♂ flowers on an indeterminate growing raceme. They showed that auxins produced in young fruits enlarge the sinkactivity of these fruits resulting in a stronger competition with differentiating flower buds for nutritious and hormonal substances. Essential for pistil development were cytokinins produced in the roots.

Tiedjens (1928) reported that removal of all ♀ flowers of (monoecious) cucumber plants (*Cucumis sativus* L.) led to an increase in the proportion of ♀ flowers. Joshi (1939) found that removal of young fruits and ♀ flowers from the protogynous inflorescence of bananas (*Musa paradisiaca* L.) lengthened the ♀ phase or led to a rhythmic flowering with ♀ and ♂ phases.

Benseler (1969) halved inflorescences of andromonoecious *Aesculus californica* (Spach) Nutt. at various times until shortly before anthesis. All treatments resulted in an increase of ☿ flowers in the lower cincinni, where few ☿ flowers were normally formed. The total number of ☿ flowers of halved inflorescences corresponded with that of entire inflorescences.

5.4.2. *Materials and methods*

Most specimens used in the experiments flowered protogynously, namely

A. pseudoplatanus 'Costorphinense' (no. 8382), 'Leopoldii' (no. 11460), 'Nervosum' (no. 17859), 'Prinz Handjery' (no. 11356), 'Purpureum' (no. 11464) and no. 8385, *A. platanoides* 'Globosum' (no. 11454) and 'Faassen's Black' (no. 13163) and *A. ginnala* (no. 12481). Two protandrous specimens concerned *A. pseudoplatanus* no. 17717 and *A. spicatum* no. 12290.

With a pair of tweezers flower buds or parts of inflorescences were removed. This concerned (at least) as many buds as ♀ flowers could be expected, all flower buds except the smallest ones or the whole inflorescence except the lowest pair of secundairy axes (with or without their terminal flower buds). The treatment started just after the bursting of the mixed buds and was performed daily until the start of anthesis. Per day inflorescences of one or some branches were treated. When more experiments were made on the same specimen the treatments were more or less randomized. In most experiments inflorescences of the same size were chosen. When their size varied equal numbers of large, medium-sized and small inflorescences were taken, while, depending on these sizes, different numbers of flower buds were removed.

5.4.3. *Results*

With protogynous *A. pseudoplatanus* specimens, removal of as many (♀) buds as ♀ flowers could be expected during the first ten days after bud break caused differentiation of the remaining largest buds into ♀ flowers. The number of newly developed ♀ flowers varied per specimen. On specimens with a low mean number of ♀ flowers per inflorescence, e.g. 'Leopoldii' and 'Purpureum' this new development did not reach the normal level. By contrast specimens with a high mean number even produced more ♀ flowers after bud removal than normal, e.g. 'Costorphinense' and 'Nervosum' (see table 22).

The new development of ♀ flowers decreased in 'Leopoldii' in the treatments on the 4th and 5th days after bud burst, while in 'Costorphinense' and no. 8385 (see table 24) this decrease was found in inflorescences treated from the 7th to 9th and from the 8th to 11th days after bud burst.

Removal of flower buds except about 10 of the smallest ones resulted in similar effects as described above (see table 23). The number of developed ♀ flowers was lower than in the first experiment.

Sometimes the inflorescences produced a second phase of ♀ flowers after the largest remaining buds (were already) differentiated into $♂_{II}$ flowers. In addition it can be said that this was particularly observed when 1 or 2 ♀ buds were mistakenly left on the inflorescence.

Reduction of the inflorescences to the lowest pair of secondary axes did not cause any increase in the number of the ♀ flowers (see table 24). Removal of both terminal buds led to the development of more ♀ flowers when the treatment was done during the first 9 days after bud burst. Removal of one terminal bud resulted in a smaller reaction which decreased in inflorescences treated 8–10 days after bud burst. A further analysis of the latter experiment shows that the secondary axis with the terminal flower gave the same response to the treatment as those of reduced inflorescences, on which both terminal flowers

TABLE 22. Sex expression of mutilated inflorescences of some protogynous *Acer pseudoplatanus* specimens, of which the ♀ flower buds were removed at various times after the bursting of the mixed buds.

cultivar and garden number Wag. B.G.	date of treatment	mean number of removed flower buds per inflorescences	number of inflorescences	mean number of flowers per inflorescence	
				♀	♀ second phase
'Costorphinense'	*1970*				
no. 8382	4/5	21	10	11.6	
	8/5	13	10	–	
	control		19	13.0	
	1971				
	20/4	8	10	14.6	
	21/4	8	10	12.2	
	22/4	8	8	13.1	
	23/4	8	14	12.8	0.1
	24/4	8	9	12.2	
	25/4	8	10	9.1	
	26/4	8	17	6.5	
	27/4	8	7	2.6	
	28/4	8	8	1.1	0.1
	29/4	8	8	1.0	
	30/4	8	9	0.6	
	2/5	8	9	1.0	
	4/5	8	11	0.4	
	5/5	8	11	0.3	
	control		50	8.8	
'Leopoldii'	*1970*				
no. 11460	4/5	8	17	3.6	0.4
	5/5	8	14	1.7	0.3
	6/5	8	14	0.1	
	7/5	8	34	–	
	control		25	4.5	
	1971				
	20/4	10	10	3.8	
	21/4	8	9	4.8	0.3
	22/4	8	10	4.3	0.8
	23/4	8	9	0.9	
	24/4	8	9	–	
	25/4	8	10	0.1	
	26/4	8	12	0.3	
	27/4	8	10	0.1	
	28/4	8	9	0.1	
	29/4	8	10	–	
	control		17	5.6	
'Nervosum'					
no. 17859	8/5	13	10	12.5	
	control		10	10.6	
'Purpureum'	6/5	13	10	3.9	
no. 11464	8/5	6	10	3.5	
	control		25	6.3	

TABLE 23. Sex expression of mutilated inflorescences of some protogynous *Acer pseudoplatanus* specimens, of which the inflorescences were reduced to the 5–15 smallest buds at various times after the bursting of the mixed buds.

cultivar and garden number Wag. B.G.	date of treatment (1971)	number of inflorescences	mean number of flowers per inflorescence		
			♀	♂$_{\mathrm{II}}$	♀(second phase)
’Costorphinense’					
no. 8382	20/4	7	4.1	4.1	
	21/4	11	5.5	3.5	
	22/4	12	5.0	4.4	
	23/4	7	3.7	0.9	0.1
	24/4	10	5.9	2.4	
	25/4	6	4.2	8.0	
	26/4	8	3.5	5.6	
	27/4	10	0.9	6.5	
	28/4	9	1.2	4.8	
	29/4	9	0.4	4.4	0.1
	30/4	8	0.1	7.4	
	2/5	7	–	4.3	
	4/5	7	–	5.0	
	5/5	7	–	6.3	
	control	50	8.8		
’Leopoldii’					
no. 11460	20/4	16	2.0	4.4	0.3
	21/4	9	1.9	4.7	0.2
	22/4	7	1.9	1.7	
	23/4	5	1.0	3.8	
	24/4	7	–	5.7	0.1
	25/4	7	–	4.0	
	control	17	5.6		

were left. By contrast, the secondary axis with the removed terminal bud showed a similar reaction as observed on reduced inflorescences without both terminal flower buds. It can be concluded that the treatment of one side axis during the first 7 days after bud burst had no influence on the sex expression of the other axis.

Removal of all ♂$_{\mathrm{I}}$ flower buds of protandrous *A. pseudoplatanus* (no. 17717) did not influence the further course of flowering and the mean number of ♀ flowers. Besides these *A. pseudoplatanus* specimens only *A. spicatum* (no. 12290) showed a similar effect: removal of all flower buds except the smallest ones resulted in the development of some ♀ flowers during the ♂$_{\mathrm{II}}$ phase of the untreated inflorescences.

Like *A. spicatum*, *A. ginnala* also flowers 4-6 weeks after bud break. However bud removal had no effect, which is the more remarkable because the specimen studied already produced a second ♀ phase spontaneously in untreated inflores-

TABLE 24. Sex expression of mutilated inflorescences of some protogynous *Acer pseudoplatanus* specimens, of which the inflorescences were reduced to the lowermost pair of secondary axes at various times after the bursting of the mixed buds.

cultivar and/or garden number	date of treatment	mean number of flowers on the two lowermost secondary axes							
Wag. B.G.		without terminal buds		with one terminal buds		with terminal buds		untreated inflorescences	
		♀	♂	♀	♂	♀	♂	♀	♂
'Nervosum'[1] no. 17859	8/5/70	2.0				2.0		2.0	
'Prinz Handjery'[2] no. 11356	12/5/70	3.2				2.0		2.0	
no. 8385[3]	23/4/71	4.3	8.3	3.5	7.5	2.6	8.7		
	24/4/71	4.8	8.7	3.4	10.7	2.7	7.9		
	25/4/71	4.8	5.4	4.0	8.1	3.4	11.0		
	26/4/71	4.1	6.8	3.7	8.4	2.8	9.5		
	27/4/71	4.3	7.9	3.9	9.3	3.1	13.0		
	28/4/71	4.1	8.2	3.6	8.1	2.8	9.8		
	29/4/71	5.0	6.6	3.9	8.6	2.9	10.6		
	30/4/71	4.2	7.7	2.3	8.7	3.1	9.5		
	2/5/71	4.1	7.4	2.2	7.6	3.1	8.6		
	4/5/71	1.3	9.4	2.7	9.3	2.7	9.7		
	6/5/71	0.5	11.4	1.7	8.7	3.2	10.2		
	8/5/71	0.9	9.8	1.4	10.1	2.7	9.7		
	average of all experiments			1.5[4]	4.7[4]	2.9	10.0	2.8	10.3

[1] number of inflorescences 18, 16 and 40 respectively

[2] number of inflorescences 14, 16 and 10 respectively

[3] 9–10 inflorescences per experiment; control 31 inflorescences

[4] axis with the terminal bud only

cences. A possible cause may be that the injuries of the inflorescences by flower bud removal just after bud burst strongly effected the competitive power with the vegetative parts. The young inflorescences were very tender.

Such early flowering species as *A. platanoides* were unsuitable for this kind of research because flowering starts immediately after bud break.

5.5. IN VITRO CULTURE OF FLOWERS AND FLOWER BUDS

After unsuccessful attempts to grow undifferentiated inflorescences (*A. maximowiczianum*) and flower buds (*A. pseudoplatanus*), taken before bud burst, in a sterile culture, undifferentiated flower buds and ♀ flowers, taken after bud break, were grown in vitro for only 8–14 days. To a sterilized Knop-nutrient[4] 15 g/l 'Chrysal' (Fa. Bendien, Naarden, The Netherlands; contains sugars, a bactericide and a fungicide) was added and further 10^{-7} M GA_3, NAA and kinetin (6 furfurylamino purine). The desinfected plant material was placed on a perforated perspex plate in Petri dishes, (diam. 17 cm) which were transferred to climate chambers at 20 ° or 25 °C, continuous illumination from fluorescent tubes and 70% humidity.

Undifferentiated flower buds of *A. ginnala* (no. 12481), *A. pseudoplatanus* (nos. 8385, 12287, 17651 and 17717) and *A. tataricum* (no. 15495), taken after bud burst and just before sex differentiation, flowered ♂ or aborted after some pistil development. Abortion was most evident in one experiment with *A. ginnala* flower buds all flowering ♂ in destilled water. The effects of phytohormones were not clear. GA_3 appeared to favour a differentiation to ♂$_{\text{II}}$ flowers, while NAA probably stimulated pistil development. It was found that only early pistil abortion led to a ♂ sex expression. The developing pistil clearly inhibits a further development of the androecium during this stage, while pistil development itself requires optimal conditions. Lack of such conditions also reduced the number of ♀ flowers per inflorescence in the experiments with detached branches (see 5.2).

The absence of any hormonal effect on this inhibition of the androecium in these and other (see 5.2) experiments may point to an inhibitor produced by the pistil which suppresses the development of the androecium shortly before anthesis (see 5.7.4).

Female flowers of *A. campestre* (no. 17163), *A. ginnala* (no. 12481) and *A. pseudoplatanus* (nos. 8385 and 17651) were used to study the functional male sterility. Phytohormones were found to have no influence.

A. macrophyllum (no. 1779) developed protogynous flowers in all treatments in the same way as observed outdoors.

5.6. VIABILITY OF POLLEN

The anthers of ♀ flowers contain pollen which was found to be rather irregular and somewhat smaller than that of ♂ flowers (see 2.8).

MUSTARD, LIU and NELSON (1954) studied pollen of ♂ and ♀ flowers of *Litchi chinensis* Sonn. (*Sapindaceae*) see also 3.4). They found that the pollen of ♂$_{\text{I}}$ flowers was less viable than that of ♂$_{\text{II}}$ flowers (germination percentages 6–45

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[4] W. KNOP (1860): quotation V. J. KONINGSBERGER (1963). Inleiding tot de plantenphysiologie, 2: 18.

and 30–66 respectively). Pollen of the closed anthers of ♀ flowers hardly germinated (0.2–0.8 %).

Pollen of 53 species and varieties of *Acer* was studied by Foster (1933). He found very high percentages of sterile pollen in the case of *A. tegmentosum* (100 %), *A. barbinerve* (90 %) and *A. spicatum* (55 %). Most of the remaining species had more than 80 % viable pollen. He supposed a possible hybrid origin in the case of the former species.

Gershoy and Gabriel (1961) described a technique developed for germinating pollen of the sugar maple (*A. saccharum*). They noted two sizes of fertile pollen grains, both in ♂ and ♀ flowers. The larger grains were characterized by thin walls, the smaller by thicker walls. From both types of flowers 25 per cent or more of pollen was empty or had disorganized contents. The authors did not specify differences in germination between ♂ and ♀ flowers.

In the present study pollen of ♂$_{\mathrm{I}}$ and ♀ flowers of *A. campestre* 'Nanum' (no. 1766) was tested using the medium of Gershoy and Gabriel. Pollen of ♀ flowers was not germinable, while only 10 % of the irregular pollen of the ♂$_{\mathrm{I}}$ flowers germinated. Pollen of ♀ flowers of *A. campestre* 'Elsrijk' (no. 17863) was also not viable, while about 80 % of pollen of ♂$_{\mathrm{II}}$ flowers developed pollen tubes. Of *A. platanoides* 'Charles F. Irish' (no. 18079) pollen was taken from closed anthers of ♀ and ♂$_{\mathrm{II}}$ flowers. The anthers of the latter would release pollen within 1–2 days. The pollen never germinated.

The ♀ flowers of *A. macrophyllum* (no 1779) sometimes shed pollen at the end of anthesis (see pag. 90). It was found to be sterile, while 20 % of pollen of ♂$_{\mathrm{II}}$ flowers germinated.

Pollen of ☿ flowers of *A. rubrum* (no. 1757) was found to be viable, germination percentages for ☿ and ♂$_{\mathrm{II}}$ flowers were 10 and 50 respectively.

5.7. DISCUSSION AND CONCLUSIONS

5.7.1. *Preliminary remarks*

The experiments provided several data which contribute to a better understanding of sex differentiation in *Acer*. Forcing of detached branches into flower gave information on the differentiation of ♂$_{\mathrm{I}}$ flowers (see 5.7.2). Under optimum forcing conditions there is no extension of the number of ♂$_{\mathrm{I}}$ flower buds during the experiment. The extent of the ♂$_{\mathrm{I}}$ phase at anthesis showed the progress of differentiation into ♂$_{\mathrm{I}}$ flower buds outdoors at the beginning of the experiment. A suboptimal development led to a decrease in the total number of flowers per inflorescence by abortion of the smallest flower buds. The mean number of ♀ flowers per inflorescence always remained lower than outdoors in those cases where a comparison was possible (flowering type C outdoors).

The addition of GA_3 or NAA to the medium led to breaking of dormancy only and did not effect sexual expression. They gave a better development and accelerated flowering compared with untreated branches, particularly when the experiments were made more than two months before the appearance of the foliage outdoors. During early spring the effect decreased and finally became negative: the branches withered after some weeks of quick development, particularly at the higher concentrations.

Breaking the dormancy by GA$_3$ was reported by Larsen (1958) for *A. rubrum*, by Irving and Lamphear (1967) for *A. negundo* and by De Maggio and Freeberg (1969) and Simsikova (1969) for *A. pseudoplatanus*. Other papers deal with phytohormones isolated from the sap of *Acer* ssp. during early spring: Nitsch and Nitsch (1965) found cytokinins and auxin in the case of *A. saccharum*; Sembder, et al. (1968) found a glycoside of GA$_8$ in *A. platanoides*.

The effects of defoliation during flower induction were most evident when developing fruits were present. In this case the further development was delayed, which led not only to a later bud burst and start of anthesis but also to a smaller ♂$_{\mathrm{I}}$ phase in protandrous *A. platanoides* (see 5.7.2).

The removal of ♀ buds during the first few days after bud burst of *A. pseudoplatanus* clearly showed the competitive power of these buds and the short period in which the ♂$_{\mathrm{II}}$ flowers are differentiated (see 5.7.3). Similar experiments with species flowering immediately after bud burst (*A. platanoides*) remained unsuccessful. This may be caused by termination of differentiation before bud break already.

The functional male sterility, i.e. the incapacity of ♀ flowers to release pollen could not be broken by hormonal treatment of isolated ♀ flowers. Pollen of the latter was never found to germinate.

Pistil development in undifferentiated flower buds grown in vitro was insufficient. Early pistil abortion either favoured a development of the androecium (♂$_{\mathrm{II}}$ flowers), or resulted in asexual flowers (see 5.7.4).

5.7.2. *Differentiation of primary ♂ flowers*

During a distinct period before anthesis pistil development in the oldest flower buds of protandrous and male flowering specimens stagnates leading to pistil abortion. The number of ♂$_{\mathrm{I}}$ flowers differentiated in this way depends on the duration of this period and the stage of development of the flower buds. The point of time of this differentiation was studied by forcing detached branches into flower at different intervals during the winter months. An optimal development of detached braches gives a good picture of the progress of differentiation into ♂$_{\mathrm{I}}$ flower buds outdoors at the beginning of the experiment.

The addition of GA$_3$ and NAA had no significant influence on sex expression. Pistil abortion is irreversible, the change from the ♂$_{\mathrm{I}}$ to the ♀ phase is always abrupt without intersexual stages.

Time and duration of this first differentiation period considerably varied with the specimens studied. In specimens of early flowering species with large inflorescences differentiation of ♂$_{\mathrm{I}}$ flower buds also started relatively early, for instance with *A. macrophyllum*, *A. platanoides* and *A. pseudoplatanus* in the beginning of January, 3.5–5 months before anthesis. By contrast, in specimens of *A. grosseri* and *A. maximowiczianum*, which have small racemose inflorescences, ♂$_{\mathrm{I}}$ flowers differentiated during April, within one month of flowering

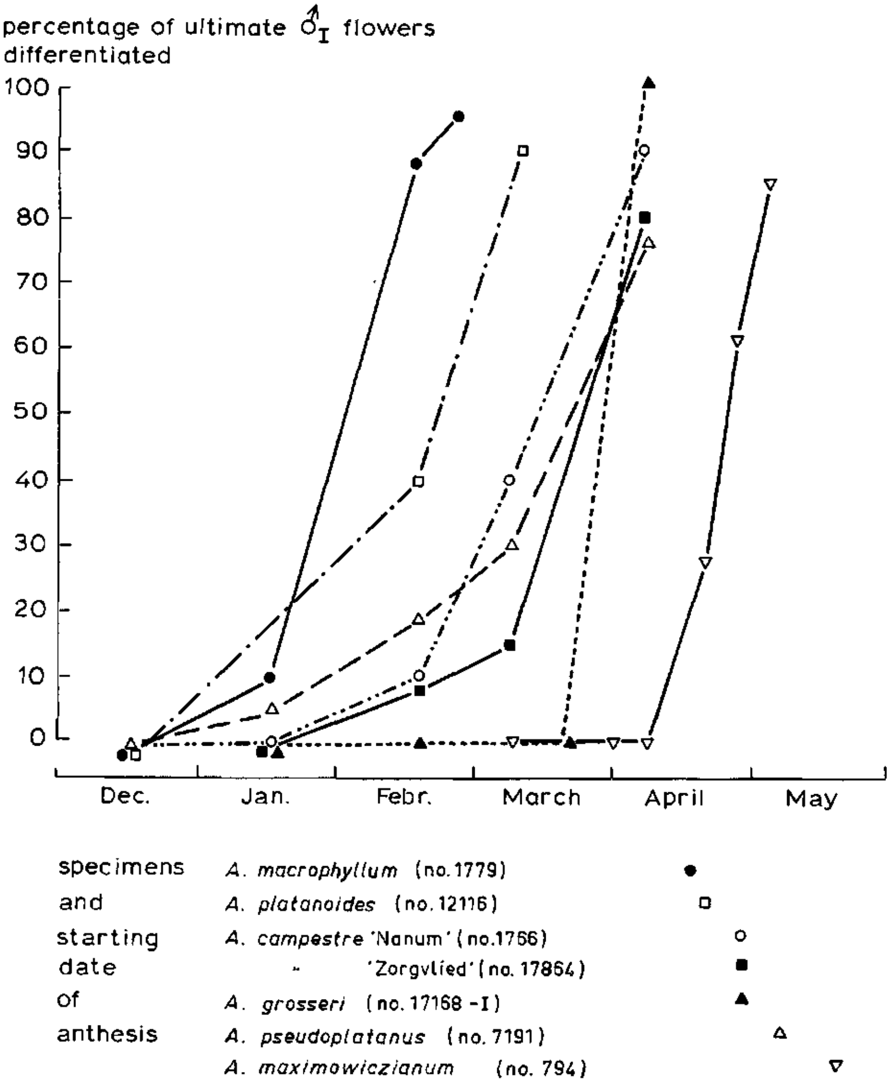

FIG. 34. Course of sex differentiation of ♂I flower buds as found after forcing of detached branches.

only. So the duration of this first differentiation period strongly varied from less than 3 weeks in the latter species to more than 3 months in *A. pseudoplatanus*. This variation is shown in fig. 34.

The delay in flower bud development after defoliation was responsible for the fact that fewer flower buds were in the stage of development in which pistil abortion occurred during the first differentiation period. Such a retarded development may also have led to the occurrence of ♀ flowers on branches of poor appearance as described in chapter 3 for the male flowering *A. campestre* 'Nanum' (no. 1766) and *A. maximowiczianum* (no. 794,) and the heavy-fruiting *A. pseudoplatanus* (no. 11480) (see pag. 55, 77, and 43). The pattern of predominantly ♂ and ♀ flowering branches as observed in the series *Tegmentosa* may be caused in some cases by competition of the fruits, which delayed flower bud induction and development on the fruit-bearing branches. This delay could lead to an escape from pistil abortion in the following spring.

The cause of pistil abortion during this phase is unknown. Abortion only occurs with pistils in a distinct stage of development and in a distinct period before anthesis, while under forcing conditions pistil development proceeds normally. During this period the mixed buds show some swelling and the dormancy of the branches rapidly decreases. In the previous chapter it was indicated that the flower buds show some development throughout the winter period. It may be possible that in the first critical period for pistil development the pistil is not able to keep pace with the growth of other floral parts by lack of essential hormones. The supply of these hormones may be hampered by dormancy of the branches and by competition of other floral parts and flower buds.

A. W. de Jong and Bruinsma (1974b) showed that specific cytokinins were required for the final cell divisions in the pistils of flowers of *Cleome ibiridella* Welw. ex Oliv.. In their studies in vitro zeatin and benzylaminopurine proved to be far more active in pistil development than kinetin and the natural cytokinin isopentenylaminopurine. Negi and Olmo (1972) previously reported that cytokinins accelerated meiotic divisions in pistillate tissue of flower buds of male *Vitis vinifera* L.

Cytokinins, which are produced in the roots, are present in the sap of *Acer spp.* (Nitsch and Nitsch, 1965). Maple sap flows during thaws from late autumn on. Sap flow prior to January is usually in small amounts and low in sugar content (Winch and Morrow, 1962).

Protogynous specimens may lack this first critical phase as a result of a much slower and more harmonious development of the largest flower buds and a sufficient hormonal supply.

According to the observations of Anderson (1964) and Taylor (1920) on the meiosis in the anthers of various *Acer* species, differentiation of ♂$_{\mathrm{I}}$ flowers takes place before this meiosis.

In species which flower more than 6 weeks after the unfolding of the leaves another mechanism may be involved in the production of ♂$_{\mathrm{I}}$ flowers; the mechanism has been studied in duodichogamous flowering *Aesculus* species. A strong competition was observed between the flower buds before anthesis leading to ♂$_{\mathrm{I}}$ flowers. Benseler (1969) found that in halved inflorescences of *Aesculus californica* (Spach) Nutt. ☿ flowers were present in cincinni, which normally produce only ♂ flowers. Unpublished experiments of the present author with the July-flowering *Aesculus parviflora* Walt. showed that inflorescences, reduced to the lowest cincinni during May, started anthesis with ☿ flowers. These ☿ flowers appeared several days later in normal inflorescences.

Halved inflorescences were intermediate with a shorter ♂$_{\mathrm{I}}$ phase and a somewhat earlier appearance of their ☿ flowers than normally.

5.7.3. *Differentiation of (primary) ♀ flowers*

Pistil development during the last few weeks before anthesis is accompanied by inhibition of stamen development. At anthesis the filaments fail to elongate and the anthers remain closed: functional male sterility. Pollen was found not to germinate in the species studied, except with some *A. rubrum* specimens, which produced ☿ flowers. Among the pollen of *A. saccharum* germinated by GERSHOY and GABRIEL (1961) possibly also pollen of ♀ flowers was involved. Pollen of ♀ flowers was found to be more heterogenous and somewhat smaller in diameter than that of ♂ flowers (see 2.8), but FOSTER (1933) and GERSHOY and GABRIEL also reported about considerable portions of sterile pollen in ♂ flowers.

The experiments with in vitro culture of undifferentiated flower buds and ♀ flowers provided some useful information on the factors controlling male sterility. All treatments of the undifferentiated flower buds were not optimal for pistil development and resulted in ♂$_{\mathrm{II}}$ and asexual flowers. Flower buds of *A. ginnala*, cultured in distilled water only, all differentiated into ♂$_{\mathrm{II}}$ flowers. All in vitro treatments of ♀ flowers to remove male sterility were unsuccesful, but in the case of *A. macrophyllum*, which sometimes developed protogynous flowers outdoors, the same treatments all resulted in a ☿ sex-expression. The occurrence of bisexuality outdoors concerned a few specimens of some species and was mostly observed in more than one year. Besides the genetic background of these trees environmental conditions did not lead to an extension of this phenomenon to other trees.

The functional male sterility is possibly due to an inhibitor produced by the pistil and does not seem to be caused by competition of the pistil (e.g. sink-activity). It seems unlikely that a final development of the nearly completed androecium of the ♀ flower buds takes so much energy that this male sterility is necessary for pistil development. The inhibition of stamen development does not immediately lead to abortion. Early, and even late, pistil abortion led to continued grow of the androecium, i.e. differentiation to ♂$_{\mathrm{II}}$ flowers.

The functional ♀ flower in *Acer* may have developed from an originally protogynous flower by strengthening of protogyny, which finally inhibited pollen release. Protogynous flowers occur in related genera, e.g. *Aesculus* (*Hippocastanaceae*).

5.7.4. *Differentiation of secondary ♂ and ♀ flowers*

The strong competition of the flower buds, which ultimately will form the ♀ phase, leads to a second critical period during which pistil abortion occurs. This abortion gives rise to the differentiation of a second phase of ♂ flowers, which have their anthesis after the ♀ phase: the ♂$_{\mathrm{II}}$ phase.

Removal of the ♀ buds at various times after bud break not only supplied information on this competition but also on the moment of differentiation of

♂$_{II}$ flowers. The experiments with *A. pseudoplatanus* showed, depending on the specimens under study, a 1–3 days lasting decrease in the development of new ♀ flowers between the 4th and 12th day after the bursting of the mixed buds. This rapid decrease illustrates the quick expansion of pistil abortion (see table 22).

The first pistils to abort are not those of flower buds following immediately after those of the ♀ phase in stage of development and anthesis but those a little further on. The observations on flowering already showed that sex differentiation on the borderline of the ♀ and the ♂$_{II}$ phase can take place very shortly before anthesis. The expansion of pistil abortion to the smallest buds mostly occurs within 1–3 days. Low temperature may retard this process.

The development of a second phase of ♀ flowers indicate the escape of an abortion by the smallest buds, especially those which are the furtherst removed from flower buds of the first ♀ phase. The experiments, in which the inflorescences were reduced to the lowermost pair of secondary axes showed that the ♀ terminal bud of one axis had no influence on the new development of ♀ flowers on the other axis (see table 24). In the case of a spontaneous occurrence of a second ♀ phase these flowers were mostly arranged at a certain distance from those of the first ♀ phase (see fig. 8 and 28). Obviously, the competative power of the ♀ buds shows relations with the distance to the undifferentiated flower buds.

This competition between flower buds for nutritive and hormonal supply especially concerns pistil development because of the meristematic activities of this floral part. Cytokinins proved to be important at this stage. A. W. DE JONG and BRUINSMA (1974b) demonstrated with the aid of in vitro culture the need of cytokinins for pistil development of undifferentiated flower buds of *Cleome iribidella* Welw. ex Oliv. They also reduced pistil abortion in *Cleome spinosa* L. by addition of cytokinins (1974c).

Probably the strong parthenocarpic tendency in *Acer* causes pistil abortion, because it is accompanied by a very quick development of the ovary, which already starts before anthesis and is completely independent of anthesis and fertilization of the egg cell. This strong parthenocarpic development may disturb the pistil development of smaller buds by its strongly increased sink activity.

The limitation of the ultimate ♀ phase also depends on the variation in stage of pistil development within an inflorescence. Removal of ♀ buds of protogynous specimens usually resulted in an increase of new ♀ flowers by the much smaller variability in the stage of pistil development of the largest remaining buds.

6. TAXONOMY

6.1. HISTORICAL SURVEY OF GENUS AND FAMILY

The genus *Acer* was founded by TOURNEFORT in 1719. LINNAEUS already accepted *Acer* as a distinct genus in the first edition of his Genera Plantarum (1737). In 1753 he described 9 species in it, of which *A. pseudoplatanus* is generally accepted as the type species.

The first monographs on the genus were made by LAUTH (1781), THUNBERG (1793) and SPACH (1834). PAX produced two monographs, which were published in 1885–1886 and 1902. The latter publication included 114 species in 13 sections.

Recently MURRAY (1970) published a monograph on the *Aceraceae*, accepting in *Acer* 7 subgenera, 24 sections, 34 series and about 120 species.

Various taxonomic studies concerned taxa of distinct areas of the genus: e.g. N. America: SARGENT (1891, 1902); China: FANG (1939, 1966), HU and CHENG (1948); Corea: NAKAI (1915); Europe: GAMS (1925), WALTERS (1968); Indochina: GAGNEPAIN (1950); Iran: MURRAY and RECHINGER (1969); Japan: THUNBERG (1784), MIQUEL (1867), KOIDZUMI (1911), OGATA (1965); Malaysia: BLOEMBERGEN (1948); Nepal: BANERJI and DAS (1971); Turkey: YALTIRIK (1967); USSR: POJARKOVA (1933, 1949).

Further studies on the genus were published by e.g.: BEAN (1970), DESMARAIS (1952), ELLIS (1969), ERRICO (1957), KELLER (1942), KOCH (1869), KRÜSSMANN (1960), LIPPOLD (1968), MAXIMOWICZ (1880), MOMOTANI (1961, 1962), NICHOLSON (1881), OGATA (1967), REHDER (1905, 1907, 1927, 1933, 1949, 1960), SCHNEIDER (1907, 1909), SCHWERIN (1893, 1903) and WESMAEL (1890).

Discussions on the delimitation of the genus mainly concerned *A. negundo*. Several authors placed this species in a separate genus *Negundo* (BOEHMER, 1760; DECANDOLLE, 1824; ENDLICHER, 1836–1840; BENTHAM and HOOKER, 1862; NIEUWLAND, 1911; PLOWMAN, 1915. RAFINESQUE (1833) proposed the name *Negundium* for this genus. More recently HALL (1951) and TOWERS and GIBBS (1953) also advocated a generic status of this taxon. NIEUWLAND (1911) and SMALL (1933) placed some other taxa in separated genera, but their view was not generally accepted.

The name *Aceraceae* was first used by LINDLEY (1836) as a name for an order. Although JUSSIEU (1789) proposed the name '*Acera*' for the family, he may be considered as the founder of the family according to Article 18 of the International Code of Botanic Nomenclature (STAFLEU, 1972).

Most authors accepted this family, including besides *Acer* the small genus *Dipteronia* Oliv. with two species in S.W. China. For some time *Dobinea* Hamilton (*Sapindaceae*) was also reckoned among the *Aceraceae* (DON, 1825; ENDLICHER, 1836–1840; BENTHAM & HOOKER, 1867).

Some authors included the *Aceraceae* in the *Sapindaceae* (REICHENBACH,

1828, 1834; HORANIVOV, 1847; GRAY, 1858; BRAUN, 1858; DRUDE, 1887).

Palynological studies by MULLER and LEENHOUTS (1976) showed strong affinities between both families. The main morphological differences concern the bicarpellate ovaries and petals without scales of the *Aceraceae* versus tricarpellate ovaries and petals with scales of the *Sapindaceae*. Further arguments of including the *Aceraceae* in the large and heterogenous family of the *Sapindaceae* are supported by the morphological similarities of the small relict genera, *Dipteronia* (*Aceraceae*) and *Delavaya* Franch. (*Sapindaceae*).

6.2. SURVEY OF CLASSIFICATIONS

Before PAX (1885) divided the genus *Acer* into 4 groups and 14 sections other authors had already distinguished separate taxa. RAFINESQUE (1836) distinguished 6 subgenera based on the species native to N.America. KOCH (1869) divided the genus into 4 groups. MAXIMOWICZ (1880) proposed two sections, *Acer* and *Negundo*. PAX's groups were based on morphological characters of the flowers, while his sections, including their names, were mainly based on features of leaves, inflorescences and fruits. In his monograph of 1902 he only distinguished 13 sections.

REHDER (1905) added one new section, *Arguta*, but in 1949 he reduced all sections except *Negundo* to serial rank. KOIDZUMI (1911) made 5 new sections, in which only Japanese species were placed.

POJARKOVA (1933) was the first to criticize PAX's system. She divided *Acer* into 17 sections, of which 4 were new, and further distinguished 32 series.

In 1948 HU and CHENG placed *A. pentaphyllum* in the monotypic section *Pentaphylla*. MOMOTANI (1962) divided the genus into 3 subgenera, *Acer*, *Carpinifolia* and *Negundo*. In the subgenus *Acer* he arranged 13 sections, of which one, *Macrophylla*, was new. In 1966 FANG published his second revision of Chinese maples. He made one new section, *Hyptiocarpa*, and further distinguished 2 subgenera, *Acer* with 15 sections and *Negundo* with 4 sections. He also proposed 9 new series. OGATA (1967) recognized 26 sections in *Acer*, including 4 new sections: *Distyla*, *Laurina*, *Parviflora* and *Syriaca*. Not knowing of the latter arrangement MURRAY (1970) accepted 24 sections and 7 subgenera. The subgenera were mainly based on morphological differences in flowers and inflorescences (especially the arrangement of the latter on the shoots) and the sex expression (monoecious or dioecious). For distinguishing taxa of lower rank, especially series, leaf morphology provided most criteria. The flowers were only indicated by him as 4- or 5-merous. No further descriptions of sepals and petals, the number of stamens and the insertion of the latter on the honey disk. The inflorescences were superficially described as e.g. corymbose, paniculate, racemose.

The dates on morphology (chapter 2), flowering and sex expression (chapter 3), the results of studies of some of the large herbarium collections and the data on biosystematic (see 6.6) and palaeosystematic (see 6.7) gave the writer a basis for a new classification as proposed in 6.4. Some criteria for this classification will be discussed in the next paragraph.

6.3. CRITERIA FOR A NEW CLASSIFICATION

The most essential points are the limitation of the taxa and their rank. First the species concept in *Acer* and related genera should be discussed. Some authors distinguished in *Acer* complex species with several geographic subspecies or varieties, e.g. ROUSSEAU (1947), DESMARAIS (1952): *A. saccharum*; KELLER (1942): *A. glabrum*; KOIDZUMI (1911): *A. palmatum*; MURRAY (1969, 1970): *A. caesium*, *A. opalus*, *A. pentapomicum*, *A. truncatum*, and others; WESMAEL (1890): *A. negundo*, a.o. Others recognised several microspecies in such complex species as *A. campestre* (DENKOVSKI, 1973, 1974), *A. miyabei* and several other species (FANG, 1939, 1966), *A. monspessulanum* and *A. opalus* (LIPPOLD, 1966), *A. pentapomicum* (POJARKOVA, 1933).

It must be noted that none of the above mentioned authors based these species on morphological features of flowers and inflorescences, mode of sex expression or compatibility studies. Leaf characters supported most criteria besides variability of the fruits (especially the angle between the wings), the geographic distribution and, rather rarely, the preference for special habitats. Although leaves are very useful for identification, they are often extremely variable, even on the same specimen. Large variations occur as a result of age, habitat and vitality of the trees. During the season the hairiness may disappear. DANSEREAU and LAFOND (1941) and DESMARAIS (1947, 1952) studied the leaf characters of the sugar maple, *A. saccharum*, and related taxa, known as *A. floridanum*, *A. grandidentatum*, *A. leucoderme* and *A. nigrum*. The occurrence of more than one of these taxa in the same locality had led to a great number of individuals, showing intermediate and recombining characters, which were previously described under many specific, varietal or formal names. Consequently DESMARAIS (1952) combined all these closely related taxa in one species, *A. saccharum* with the above (mentioned) taxa as subspecies. These combinations were accepted by MURRAY (1970).

The present author agrees to consider such complex and variable taxa as one species when they show strong resemblances in their reproductive organs. This resulted in a rejection of some of MURRAY's combinations: *A. cissifolium* and *A. henryi*, *A. decandrum* and *A. laurinum*, *A. mono* and *A. truncatum*.

Of several taxa, especially from Asia, lack of herbarium and cultivated specimens made taxonomic revisions difficult, because within complex taxa variations and affinities are insufficiently known. As a consequence many taxa of these areas are adopted as species which may prove to be untenable.

The limited number of morphological characters on which PAX (1885) based his sections has led to much revision. POJARKOVA (1933), MOMOTANI (1962) and OGATA (1967) tried to propose a more natural division but their incomplete knowledge of the genus, especially of the morphology and of a number of taxa, limited the results. MURRAY (1970) recognized 66 intrageneric taxa, but he did not make a natural arrangement. More specialized (dioecious or anemophilous) taxa were placed in small separate subgenera, while he further distinguished several monotypic sections and series in his subgenus *Acer*. This large number of taxa strongly contrasts with MURRAY's species concept, and also with REHDER (1949), who distinguished only 2 sections, *Acer* and *Negundo*, and 14 series. The personal ideas about the rank of intrageneric taxa could lead to such divergent views.

Although the present area of *Acer* must be considered as a relict area with most taxa isolated from each other since the end of the Tertiary, a natural arrangement in a limited number of sections and series is still possible. Such a systematy may also be more in balance with classification concepts in related families, e.g. *Sapindaceae* (LEENHOUTS, 1967, 1969) and *Hippocastanaceae* (HARDIN, 1957). The present author recognizes 14 sections in *Acer*, of which 8 include 2–3 series. No subgenera are proposed, although he agrees with MOMOTANI (1962) regarding the remote relationships between *A. carpinifolium* and the remaining taxa.

6.4. PROPOSED CLASSIFICATION OF THE GENUS ACER

I. Section Acer

Type species: *A. pseudoplatanus* L. Homotypic synonyms: *Spicata* Pax, in Engler, Bot. Jahrb., 6: 327 (1885), partly (no species cited): ibid., in Engler, Bot Jahrb., 7: 182 (1886), partly (excl. *A. tataricum* L., *A. ginnala* Maxim., *A. trifidum* Hook. (= *A. buergerianum* Miq.), *A. pilosum* Maxim., *A. cinerascens* Boiss. (= *A. monspessulanum* L.), *A. spicatum* Lam., *A. macrophyllum* Pursh., *A. caudatum* Wall., (= *A. ukurunduense* Trautvet. & Meyer), *A. campbellii* Hook. f. & Thoms.); ibid., in Engler, Pflanzenreich, IV, 163: 8 (1902) partly (excl. besides the species listed above: *A. betulifolium* Maxim. (= *A. stachylophyllum* Hiern.), *A. paxii* Franchet, *A. trinerve* Dippel (= *A. buergerianum* Miq.), *A. x boscii* Spach, *A. acuminatum* Wall. ex D. Don, *A. multiserratum* Maxim., (= *A. ukurunduense* Trautv. & Meyer) *A. oliverianum* Pax, *A. erianthum* Schwerin, *A. sinense* Pax, *A. isolobum* sensu Kurz (= *A. osmastonii* Gamble), *A. pentapomicum* Stewart ex Brandis). *Gemmata* Pojarkova, Acta Inst. Bot. Acad. Sci. U.S.S.R., 1, 1:312 (1933).

Heterotypic synonyms: *Saccharina* Pax, l.c.: 328 (1885); ibid., l.c.: 241 (1886); ibid. l.c.: 77 (1902). Type species: *A. saccharinum* sensu Wangenheim non L. (= *A. saccharum* Marsh.). Homotypic synonyms: *Saccharodendron*. Rafinesque, New Flora of N. Amer., 1: 47 (1836) as subgenus. *Saccharata* Graebner, in Graebner & Lange, Illustr. Gartenbau Lexicon, ed. 4,1: 15 (1926).

Goniocarpa Pojarkova, l.c.: 347. Lectotype species: *A. monspessulanum* L. (fide Murray).

Syriaca Ogata, Bull. Tokyo Univ. For., 63:144 (1967) partly (excl. *A. pentapomicum* Stewart ex Brandis) nomen provis. Type species: *A. syriacum* Boiss. (= *A. sempervirens* L.).

Trees or shrubs, deciduous, occasionally (partly) evergreen (*A. sempervirens* L.). *Leaves* 3–5-lobed; margins coarsely crenate to dentate, sometimes entire. *Bud scales* 5–13-paired, imbricate, grey-brown. *Inflorescences* corymbose (type II), terminal and axillary. *Flowers* 5-merous; perianth yellowish-green, often somewhat closed during anthesis; stamens mostly 8, long exserted filaments in ♂ flowers; disc extra-staminal. *Fruits*: nutlets ovoid, often keeled, parthenocarpic tendency strong, sometimes moderate. *Seedlings*: cotyledons narrowly oblong; apex obtuse or truncate.

The section includes three series:

A. **Series Acer**

Homotypic synonyms: *Spicata* Pax, in Engler, Bot. Jahrb. 7: (1886) partly (excl. *A. spicatum* Lam., *A. macrophyllum* Pursh.) as *Spicati. Pseudoplatani* Pojarkova, l.c.: 312. *Gemmata* Pojarkova l.c.: 312 as section.

Heterotypic synonyms: *Trautvetterana* Pojarkova, l.c.: 312. Type species: *A. trautvetteri* Medwed.

Velutina Pojarkova, l.c.: 312. Type species: *A. velutinum* Boiss.

Trees, deciduous; young branches and buds rather thick. *Leaves* mostly 5-lobed, chartaceous; margins coarsely serrate. *Bud scales* 5–10-paired. *Inflorescences* rather big, 25–150 flowers. *Fruits*: nutlets ovoid globose, occasionally somewhat keeled, pathenocarpic tendency moderate.

Area: C. and S.E. Europe, W. Asia, W. Himalaya to N.W. China.

Species: *A. pseudoplatanus* L., *A. heldreichii* Orph. ex Boiss., *A. trautvetteri* Medwed., *A. velutinum* Boiss., *A. caesium* Wall. ex Brandis.

B. **Series Monspessulana** Pojarkova, l.c.: 355.

Type species: *A. monspessulanum* L.

Homotypic synonym: *Goniocarpa* Pojarkova, l.c.: 347 as section.

Heterotypic synonym: *Opulifolia* Pojarkova, l.c.: 347. Type species: *A. opulifolium* Villars (= *A. opalus* Mill.).

Trees or shrubs, deciduous or (partly) evergreen. *Leaves* mostly 3-, sometimes 5-, rarely unlobed, often coriaceous; margins entire to coarsely serrate. *Bud scales* 8–12-paired. *Inflorescences* with 10–50 flowers, mostly with long, drooping pedicels. *Fruits*: nutlets keeled-convex, parthenocarpic tendency strong.

Area: S. Europe, W. Asia and N. Africa.

Species: *A. monspessulanum* L., *A. opalus* Mill., *A. sempervirens* L. (syn. *A. orientale* Mill.), *A. hyrcanum* Fischer & Meyer.

C. **Series Saccharodendron** (Rafinesque) Murray, Kalmia, 2: 1 (1970)

Basionym: *Saccharodendron* Raf., New Flora of N. America, 1: 47 (1836) as subgenus.

Type species: *A. saccharum* Marsh.

Homotypic synonyms: *Saccharina* Pax, l.c.: 328 (1885) as section. *Saccharum* Pojarkova, l.c.: 240, nomen nudum.

Trees, deciduous. *Leaves* 3–5 sometimes to 7-lobed, chartaceous, margins entire to coarsely dentate. *Bud scales* 6–9-paired. *Inflorescences* with 10–60 flowers, drooping pedicels, terminal and rather frequently axillary, the latter partly from leafless buds. *Flowers* apetalous; calyx connate. *Fruits:* nutlets spherical, parthenocarpic tendency strong.

Area: Eastern N. America to C. America.

Species: *A. saccharum* Marsh., *A. skutchii* Rehder (= preceding?).

NOTES. PAX's section *Spicata* included the type species of the genus, *A. pseudoplatanus*. According to the Code this section should be called *Acer*. In its present delimitation section *Acer* includes only 5 species of PAX's section *Spicata*. These species form the series *Acer*.

The 3 series distinguished by the present author show resemblances in the morphology of their reproductive organs, leaves, bud scales and seedlings and are in his opinion closely related. These affinities were previously suggested by POJARKOVA (1933) and OGATA (1967).

Series *Acer* is synonymous with POJARKOVA's section *Gemmata*. Despite the strong affinities of the 5 species POJARKOVA proposed three series, which were accepted by MURRAY (1970). Series *Monspessulana* is synonymous with POJARKOVA's section *Goniocarpa*. Accepting MURRAY's combinations it includes 4 heterogeneous species. The deciduous taxa show some development to anemophily, having anthesis before leaf development, drooping flowers with long, thin pedicels, exserted stamens (♂) or large stigmas (♀). The evergreen taxa have small inflorescences which resemble those of series *Acer*. The nomenclature of *A. sempervirens* L. (syn. *A. orientale* Mill.) was discussed by YALTIRIC (1967) and in BEAN (1971).

Series *Saccharodendron* is synonymous with PAX's section *Saccharina*. The recognition of this taxon as a section or even as a subgenus by RAFINESQUE (1836) and MURRAY (1970) was mainly based on the apetalous flowers. In other morphological characters, however, this series strongly resemble series *Monspessulana* (see further 6.6.1, 6.6.2 and 6.7).

The strong affinities of the taxa of series *Saccharodendron* led to the combination into one complex species. *A. saccharum* by DESMARAIS (1952). This was accepted by MURRAY.

The nomenclature of *A. saccharum* is extensively discussed by MACKENZIE (1926), SUDWORTH (1926), SPRAGUE (1929) and ROUSSEAU (1940). The latter proposed *A. saccharophorum* Koch as its valid name, which was not generally accepted. However rejecting the name *A. saccharum* (as a misprint of *A. saccharinum* sensu Wangenheim, non L.) and accepting ROUSSEAU's or DES-

MARAIS combinations makes *A. nigrum* Michaux f. the oldest valid synonym. Consequently the correct name for the sugar maple must be *A. nigrum* subsp. *saccharum* (Marshall) Desmarais.

II. **Section Platanoidea** Pax, in Engler, Bot. Jahrb., 6: 327 (1885); ibid. in Engler, Bot. Jahrb., 7: 233 (1886); ibid. in Engler, Das Pflanzenreich, IV, 163: 46.

Type species: *A. platanoides* L.

Heterotypic synonyms: *Campestria* Pax, l.c.: 327 (1885) partly (no species cited); ibid., l.c.: 219 (1886), partly (excl. *A. grandidentatum* (Nutt.) Torrey & Gray (= *A. saccharum*), *A. obtusatum* Wald. & Kit. (= *A. opalus* Mill.), *A. italum* Lauth (= preceding, partly *A. hyrcanum* Fisch. & Meyer), *A. reginae-amabile* Orph. ex Boiss. (= *A. hyrcanum?*), *A. monspessulanum* L., *A. orientale* Mill. (= *A. sempervirens* L.), *A. syriacum* Boiss. (= preceding); ibid., l.c.: 54 (1902), partly (excl. besides the species cited above: *A.* × *rotundilobum* Schwerin (= *A. monspessulanum* × *A. opalus*), *A. cinerascens* Boiss. (= *A. monspessulanum*). Type species: *A. campestre* L.

Pubescentia (Pojarkova) Ogata, Bull. Tokyo Univ. For., 63: 136 (1967), Basionym: *Platanoidea* series *Pubescentia* Pojarkova, Acta Inst. Bot. Acad. Sci. U.S.S.R., 1, 1 : 307 (1933). Type species: *A. pubescens* Franch. (= *A. pentapomicum* Stewart ex Brandis).

Trees and shrubs, deciduous. *Leaves* 3-5-, sometimes 7-lobed, rarely undivided, chartaceous or somewhat coriaceous; margins entire, remotely dentate or serrate. *Bud scales* 5–8- or 6–10-paired. *Inflorescences* corymbose (type II), terminal and axillary, mostly from mixed buds. *Flowers* 5-merous, stamens 5 or 8, disc amphistaminal. *Fruits*: nutlets flat, parthenocarpic tendency moderate. *Seedlings*: cotyledons large, narrowly oblong.

The section includes two series:

A. **Series Platanoidea**

Heterotypic synonyms: *Picta* Pojarkova, l.c.: 278. Type species: *A. pictum* sensu auctorum, non Thunberg (= *A. mono* Maxim.).

Quinqueloba Pojarkova, l.c.: 278. Type species: *A. quinquelobum* Koch (= *A. divergens* Pax).

Campestria (Pax) Pojarkova, l.c.: 297. Type species: *A. campestre* L. Basionym *Campestria* Pax, l.c., partly, as section.

Catalpifolia Fang, Acta Phytotax. Sinica, 11 : 147 (1966). Type species: *A. catalpifolium* Rehder.

Fulvescentia Fang, l.c.: 144. Type species: *A. fulvescens* Rehder.

Miaotaiensia Fang, l.c.: 144. Type species: *A. miaotaiense* Tsoong (= *A. miyabei* Maxim.).

Leaves 3–5-, sometimes 7-lobed, rarely undivided, margins entire or remotely dentate, petioles lactiferous. *Bud scales* 5–8-paired. *Inflorescences* terminal, sometimes axillary. *Flowers* 8-stamened.

Area: C. Europe to E. Asia.

Species: *A. platanoides* L., *A. turkestanicum* Pax (= preceding?), *A. cappadocicum* Gled., *A. lobelii* Tenore (= preceding?), *A. divergens* Pax, *A. amplum* Rehder *A. acutum* Fang (= preceding?), *A. catalpifolium* Rehder, *A. chunii* Fang (= preceding?), *A. longipes* Franchet, *A. fulvescens* Rehder (= preceding?), *A. pashanicum* Fang & Soong (= preceding?), *A. mono* Maxim., *A. truncatum* Bunge, *A. okamotoanum* Nakai (= preceding)?, *A. tenellum* Pax, *A. tibetense* Fang, *A. campestre* L., *A. miyabei* Maxim, *A. chapaense* Gagnepain.

B. Series Pubescentia Pojarkova, l.c.: 307.

Type species: *A. pubescens* Franchet (= *A. pentapomicum* Stewart ex Brandis).

Leaves 3-lobed, somewhat coriaceous, glaucous beneath; margins coarsely serrate; petioles not lactiferous. *Bud scales* 6–10-paired. *Inflorescences* axillary and terminal, the former partly from leafless buds. *Flowers*: petals somewhat rolled inwards; stamens mostly 5.

Area: C. Asia, N.E. China.

Species: *A. pentaponicum* Stewart ex Brandis, *A. pilosum* Maxim.

NOTES. The delimitation of section *Platanoidea* is according to POJARKOVA (1933). The two series show resemblances in the morphology of their reproductive organs. They are probably rather remotely related.

Series *Platanoidea* is a very natural group of closely related species. PAX's arrangement of *A. campestre* and *A. miyabei* in section *Campestria* was first criticized by WARSOW (1903), who studied the leaf anatomy. There is no need for more series as proposed by POJARKOVA and FANG (1966), not even for a series *Campestria* as accepted by MOMOTANI (1962), OGATA (1967) and MURRAY (1970). MURRAY recognized 17 species in series Platanoidea. This number may further decrease by future revisional work, especially, when several Chinese taxa are better known. *A. lobelii* is very close to *A. cappadocicum*. Both show the same typical bark stripes, while their flowers and fruits are very similar. *A. divergens* also shows affinities to *A. cappadocicum*. *A. turkestanicum* is very close to *A. platanoides*. They have similar flowers and fruits. Combinations of the above mentioned taxa are more rational than MURRAY's combination of *A. truncatum* and *A. mono* (1969). These species vary in their bark (split and lenticellulate respectively); the time of anthesis, their flowers and the germination of the seeds (see 2.6.3).

Series *Pubescentia* forms a more specialised group than series *Platanoidea*. The arrangement of the inflorescences is clearly shifting to axillary positions, while the androecium is reduced to one whorl. After studying the variable taxa of C. Asia the present author agrees with MURRAY's adoption of only one species, *A. pentapomicum*. POJARKOVA (1949) first understood the affinities of this taxon with *A. pilosum* from N.E. China, a species which was very little known. In MAXIMOWICZ' original description a branchlet is figured with racemose inflorescences, developed from leafless lateral buds. On account of this figure REHDER (1927) included *A. pilosum* in section *Lithocarpa* (= series *Lithocarpa*), which was adopted by MOMOTANI (1962) and MURRAY (1970).

III. **Section Palmata** Pax, in Engler, Bot. Jahrb., 6: 326 (1885); ibid., in Engler, Bot. Jahrb., 7: 198 (1886); ibid., in Engler, Pflanzenreich, IV, 163: 24.

Type species: *A. palmatum* Thunberg.

Heterotypic synonym: *Microcarpa* Pojarkova, Acta Inst. Bot. Acad. Sci. U.S.S.R. 1, 1: 339 (1933), partly (excl. *A. spicatum* Lam., *A. ukurunduense* Trautv. & Meyer), *A. caudatum* Wall. (= preceding), *A. multiserratum* Maxim. (= preceding). Lectotype species: *A. sinense* Pax (fide Murray).

Antadenium Rafinesque, New Flora of N. Amer., 1: 49 (1836) as a subgenus. Type species: *A. circinatum* Pursh.

Trees and shrubs, deciduous or (partly) evergreen, usually or often the terminal buds abortive. *Leaves* 3–13-lobed, or undivided, chartaceous or coriaceous, margins serrate, sometimes entire. *Bud scales* always 4-paired. *Inflorescences* corymbose with cincinni (type I), terminal and, less frequently, axillary, pedicels of blown ♂ flowers often partly dropped. *Flowers* 5-merous, sepals red or green-red, petals mostly white and rolled inwards, stamens 8, disc extrastaminal. *Fruits*: nutlets elliptical-globose, never empty, parthenocarpic tendency low to moderate. *Seedlings*: cotyledons narrowly oblong; apex obtuse.

The section includes three series:

A. **Series Palmata**

Heterotypic synonyms: *Pseudosieboldiana* Fang, Acta Phytotax. Sinica, 11: 148 (1966). Type species: *A. pseudosieboldianum* (Pax) Komarov.

Robusta Fang, l.c.: 149. Type species: *A. robustum* Pax.

Trees and shrubs, deciduous, terminal buds usually abortive, *Leaves* 5–9-, sometimes to 13-lobed, suborbicular, chartaceous; margins serrate. *Inflorescences* with 5–25 flowers; pedicels of blown ♂ flowers completely dropped. *Flowers*: petals sometimes reddish; stamens of blown ♂ flowers drop first. *Fruits*: nutlets mostly veined, parthenocarpic tendency moderate.

Area: N.E. Asia to C. China, western N. America.

Species: *A. palmatum* Thunb., *A. japonicum* Thunb., *A. sieboldianum* Miq., *A. shirasawanum* Koidz., *A. tenuifolium* (Koidz). Koidz., *A. robustum* Pax, *A. anhweiense* Fang & Fang f. (= preceding?), *A. ceriferum* Rehder, *A. pubipalmatum* Fang, *A. pauciflorum* Fang, *A. pseudosieboldianum* (Pax) Komarov, *A. takeshimense* Nakai (= preceding?), *A. circinatum* Pursh.

B. **Series Sinensia**, Pojarkova, Acta Inst. Bot. Acad. Sci. U.S.S.R., 1.1: 339 (1933).

Type species: *A. sinense* Pax.

Heterotypic synonym: *Tonkinensia* Murray, Kalmia, 1: 37 (1969). Type species: *A. tonkinense* Lecomte.

Trees deciduous, terminal buds often abortive. *Leaves* 3–7-lobed, chartaceous, sometimes coriaceous; margins serrate, sometimes entire. *Inflorescences* big, mostly with elongated rachis, 20–250 flowers, pedicels of blown ♂ flowers mostly partly dropped. *Flowers*: sepals often somewhat recurved; petals often lobed; disc sometimes pubescent; blown ♂ flowers probably drop anthers first. *Fruits*: parthenocarpic tendency low.

Area: C. & S. China, S. and E. Himalayas (subtropical).

Species: *A. sinense* Pax, *A. sunyiense* Fang (= preceding?), *A. prolificum* Fang & Fang f. (= preceding?), *A. campbellii* Hook f. & Thoms. ex Hiern, *A. erianthum* Schwerin, *A. kweilinense* Fang & Fang f. (= preceding?), *A. miaoshanicum* Fang (= predecing?), *A. confertifolium* Merrill & Metcalf, *A. flabellatum* Rehder, *A. gracile* Fang & Fang f. non Saporta (= preceding?), *A. lanpingense* Fang & Fang f. (= preceding?), *A. tonkinense* Lecomte, *A. fenzelianum* Handel-Mazzetti, *A. osmatonii* Gamble, *A. shangszeënse* Fang & Soong, *A. wilsonii* Rehder, *A. heptaphlebium* Gagnepain, *A. tutcheri* Duthie.

C. **Series Penninervia** Metcalf, Lingnan Sci. Journ., 11: 202 (1932) as *Penninervium.*

Lectotype species: *A. laevigatum* Wall. (fide Murray).

Homotypic synonyms: *Laevigata* Fang, l.c.: 170. *Laevigata* Ogata, Bull. Tokyo Univ. For., 63: 122 (1967), nomen superfluum.

Trees (partly) evergreen, usually terminal buds abortive. *Leaves* unlobed, coriaceous, margins entire to serrate. In other morphological characters as series *Sinensia.*

Area: S. Himalayas, S. China (subtropical).

Species: *A. laevigatum* Wall., *A. erythranthum* Gagnep. (= preceding?), *A. hainanense* Chun & Fang (= preceding?), *A. crassum* Hu & Cheng, *A. fabri* Hance, *A. sino-oblongum* Metcalf, *A. cordatum* Pax, *A. kuikiangense* Hu & Cheng (= preceding?), *A. lucidum* Metcalf, *A. reticulatum* Champ.

NOTES. In its present delimitation section *Palmata* was first recognized by OGATA (1967). Although the taxa of this section form a natural group, the section is somewhat heterogenoeus as a result of various specialisations.

A division into one series, *Sinensia*, with the more primitive taxa, and two series, *Palmata* and *Penninervia*, with more specialized taxa, is somewhat artificial on account of intermediary taxa.

Series *Palmata* includes the most specialized taxa of this section, showing a reduction of the inflorescences, a complete drop of pedicels of blown ♂ flowers, less variation between calyx and corolla, a thicker, more lignified pericarp and often a strong increase in the number of leaf lobes. They mainly occur in temperate areas.

Series *Sinensia* represents the primitive taxa. Several of these taxa are very little known. A species which may be considered as very primitive is *A. tonkinense.* It has large trilobate leaves, very large inflorescences and small flowers with reddish, somewhat recurved sepals, small, lobed, white petals and a hairy disc (see fig. 16).

MURRAY (1969) proposed a monotypic series *Tonkinensia*, mainly on the basis of the short stalked trilobate leaves. He further considered *A. fenzelianum* as conspecific. However, this species has small pilose inflorescences, large flowers with a glabrous disc and fruits with a relatively thick pericarp.

Series *Penninervia* mainly deviates from the previous series by the persistent unlobed leaves. As far as studied seedlings exclusively develop unlobed leaves.

Future revisional work will very probably strongly reduce the number of species of this section.

IV. **Section Macrantha** Pax, in Engler, Bot. Jahrb., 6: 328 (1885); ibid., in Engler, Bot. Jahrb., 7:244 (1885), partly (excl. *A. parviflorum* sensu Franch. & Savat. (= *A. nipponicum* Hara)); ibid., in Engler, Pflanzenreich, IV, 163: 67 (1902) partly (excl. *A. erosum* Pax (= *A. ukurunduense* Fischer & Meyer)), *A. parviflorum* (=*A . nipponicum*), *A. crassipes* Pax (= preceding).

Lectotype species: *A pensylvanicum* L. (fide Murray).

Heterotypic synonym: *Palmatoidea* Koidzumi, Journ. Coll. Sci. Univ. Tokyo, 32, 1: 22. Type species: *A. micranthum* Sieb. & Zucc.

Trees more often shrubs, deciduous. *Leaves* undivided or 3–5-, sometimes to 7-lobed, often caudate-acuminate; margins serrate. *Bud scales* always 2-paired, valvate, red or green-red. *Inflorescences* racemose or corymbose (types III and I respectively), terminal and axillary, 10–25 flowers. *Flowers* 5-merous; perianth green-yellow or reddish; stamens 8. *Fruits*: nutlets flat, sometimes globose; parthenocarpic tendency variable, moderate to weak.

The section includes two series:

A. **Series Tegmentosa** Pojarkova, Acta Inst. Bot. Acad. Sci. U.S.S.R. 1, 1: 345 (1933).

Type species: *A. tegmentosum* Maxim.

Heterotypic synonyms: *Crataegifolia* Pojarkova, l.c.: 345. Type species: *A. crataegifolium* Sieb. & Zucc.

Micrantha Pojarkova, l.c.: 345, partly (excl. *A. wardii* W.W. Smith). Type species: *A. micranthum* Sieb. & Zucc. Homotypic synonym: *Palmatoidea,* Koidzumi, l.c. as section.

Macrantha (Pax) Rehder, Bibliograph. of Trees and Shrubs: 424 (1949). Basionym: *Macrantha* Pax, in Engler Bot. Jahrb., 6, 328 (1885) as section. Lectotype species: *A. pensylvanicum* L.

Rufinervia Momotani, Mem. Coll. Sci. Univ. Kyoto B., 29: 180 (1962). Type species: *A. rufinerve* Sieb. & Zucc.

Maximowicziana Fang, Acta Phytotax. Sinica, 11: 176 (1966). Type species: *A. maximowiczii* Pax.

Small trees, or shrubs, branches often with white wash stripes, axillary buds stalked. *Bud scales* always 2-paired, valvate. *Inflorescences* simple racemes (type III), 10–25 flowers. *Flowers*: perianth green-yellow or green-red; disc intrastaminal. *Fruits*: nutlets convex, more often rather flat, one side convex, the other side convex with a hole in the centre or concave (seedless parthenocarpic fruits). *Seedlings*: cotyledons small, elliptic.

Area: S. Himalayas to N.E. Asia, E.N. America.

Species: *A. pensylvanicum* L., *A. tegmentosum* Maxim., *A. rufinerve* Sieb. & Zucc., *A. capillipes* Maxim., *A. morifolium* Koidzumi (= preceding?), *A. micranthum* Sieb. & Zucc., *A. tschonoskii* Maxim., *A. davidii* Franch., *A. grosseri* Pax (= preceding?), *A. laxiflorum* Pax, *A. hookeri* Miq., *A. sikkimense* Miq., *A. pectinatum* Wall ex Nicholson, *A. taronense* Handel-Mazzetti, (= preceding?), *A. forrestii* Diels (= preceding?), *A. maximowiczii* Pax, *A. metcalfii* Rehder, *A. rubescens* Hayata, A. *caudatifolium* Hayata.

B. **Series Wardiana,** ser. nov.

Type species: *A. wardii* W. W. Smith

Arbores parvae vel frutices; ramuli rigidi pilosi. Folia trilobata, margine serrulato. Inflorescentia erecta, corymbosa cum cincinnis parvis; axes secondarii oppositi; bracteae distinctissimae. Flores perianthiis rubris, reflexis sub finem anthesis; discus amphistaminalis; stamina ex floribus primo decident. Fructus nuculis mediocriter planis.

Small trees, or shrubs; young shoots with stiff hairs. *Leaves* 3-lobed, margin serrulate. *Inflorescences* upright, corymbose; with small cincinni (type I), secondary axes opposite; bracts very distinct. *Flowers*: perianth red, recurved at the end of anthesis; disc amphistaminal; blown ♂ flowers shed stamens first. *Fruits*: nutlets rather flat.

Monotypic: *A. wardii* W. W. Smith; S. and E. Himalayas.

NOTES. In its present delimitation section *Macrantha* includes two series which are very probably somewhat remotely related. Series *Tegmentosa* is a very natural group, which does not need further division as previously proposed by POJARKOVA (1933) and accepted by MOMOTANI (1962), FANG (1966), OGATA (1967) and MURRAY (1970). This division was artificially made on the basis of leaf morphology. The taxa of series *Tegmentosa* all develop trilobate leaves as young seedlings. They also hybridize very spontaneously in botanic gardens, and introgressive hybridizations may occur in the wild. Although MURRAY (1966, 1970) already combined some species, this series needs further revision (see also DE JONG, 1974). A combination of *A. davidii* and *A. grosseri*, of which intermediary types were found in the herbaria, may be preferred to MURRAY's (1966) combination of *A. grosseri* and *A. tegmentosum*. *A. forrestii* and *A. taronense* are very close to *A. pectinatum* and may probably be combined.

The monotypic series *Wardiana* is very distinct from series *Tegmentosa*. In the original description W. W. SMITH (1917) already reported on the distinctness of *A. wardii*. He mentioned the long bracts and the amphistaminal disc and suggested some affinity to *A. sinense* (series *Sinensia*). The inflorescences with small cincinni and the amphistaminal disc made that series somewhat more primitive than series *Tegmentosa.*

V. **Section Parviflora** Koidzumi, Journ. Coll. Sci. Univ. Tokyo, 32. 1: 11 (1911).

Type species: *A. parviflorum* sensu Franch. & Savat. (= *A. nipponicum* Hara).

Heterotypic synonym: *Distyla* Ogata, Bull. Tokyo Univ. Forest., 63: 115 (1967). Type species: *A. distylum* Sieb. & Zucc. *Distyla* Murray, Kalmia, 1: 41 (1969), nomen superfluum.

Trees and shrubs, deciduous. *Leaves* 3-, sometimes 5–7-lobed or undivided, chartaceous: margins serrate. *Bud scales* 2-, sometimes partly 3-paired. *Inflorescences* big, corymbose (type I), elongated rachis with cincinni, terminal and axillary, 35–400 flowers. *Flowers* 5-merous; perianth greenwhite; stamens mostly 8; disc amphi- or intra-staminal; anthesis some weeks after busting of the mixed buds. *Fruits*: pathenocarpic tendency low.

The section includes three series:

A. **Series Parviflora**

Trees, branches rather thick. *Leaves* big, 3–5-lobed, margin double serrate. *Bud scales* always 2-paired, ± valvate, green-red. *Inflorescences* very large, long drooping panicle, ferruginously pubescent, 150–400 or more flowers. *Flowers*: perianth small, glabrous; disc intrastaminal, slightly ferruginous pubescent. *Fruits*: nutlets big, globose, densily ferruginous pubescent when young. *Seedlings*: cotyledons large, narrowly oblong; apex truncate.

Monotypic: *A. nipponicum* Hara, Japan.

B. **Series Ukurunduensia,** ser. nov.

Type species: *A. ukurunduense* Trautv. & Meyer.

Arbores parvae vel frutices. Folia 3–5-lobata, interdum 7-lobata, subtus pilosa, margine serrato. Squamae gemmarum 2-binatae ex parte 3-binatae. Inflorescentia erecta floribus 50–200; pedicelli florum defloratorum masculinorum ex parte decident. Flores petalis oblongis albisque, duplicis longis sepalibus pilosis viridisque; discus lobatus, ex parte amphistaminalis.

Fructus nuculis parvis, planis nervatisque, latere altero convexo, altero mediocriter concavo. Plantulae cotyledonibus parvis, anguste ellipticis.

Small trees or shrubs. *Leaves* 3–5-, sometimes to 7-lobed, pubescent beneath, margins serrate. *Bud scales* 2-, partly 3-paired. *Inflorescences* upright, pedicels of blown ♂ flowers partly dropped, 50–200 flowers. *Flowers*: petals narrow, white, twice as long as the hairy greenish sepals; disc lobed, partly amphitaminal, partly intrastaminal; blown ♂ flowers drop petals and stamens first. *Fruits*: nutlets small, flat, veined, one side convex, the other somewhat concave. *Seedlings*: cotyledons small, narrowly elliptic.

Area: Himalaya to N.E. Asia, eastern N. America.

Species: *A. ukurunduense* Trautv. & Meyer, *A. spicatum* Lam.

C. **Series Distyla** (Ogata) Murray, Kalmia, 2: 1 (1970).

Type species: *A. distylum* Sieb. & Zucc.

Basionym: *Distyla* Ogata, Bull. Tokyo Univ. Forest., 66: 115 (1967) as section,

Trees. *Leaves* undivided, deeply cordate; margins crenate. *Bud scales* always 2-paired, valvate, brownish, pubescent. *Inflorescences* upright, ferruginous pubescent, 35–70 flowers. *Flowers*: sepals hairy; disc lobed; stamens inserted between the lobes. *Fruits*: nutlets elliptic-convex, strongly ferruginous pubescent when young. *Seedlings*: cotyledons narrowly elliptic.

Monotypic: *A. distylum* Sieb. & Zucc., Japan.

NOTES. Section *Parviflora* includes 3 not closely related series, which represent primitive relict taxa of *Acer*. In its present delimitation it was first recognized by MOMOTANI (1962). The rejection of *A. spicatum* as type species of section and series *Spicata*, which included the type species of the genus (*A. pseudoplatanus*) made *Parviflora* the oldest valid name of this section, while in the case of the series a new name, *Ukurunduensia*, must be proposed. According to MURRAY (1970) the type species of series *Caudati* Pax is *A. caudatum* sensu Pax, which is synonymous with *A. acuminatum*.

Series *Ukurunduensia* includes two very closely related species. All Asiatic taxa of this series may be combined in *A. ukurunduense*. Although MURRAY accepted *A. caudatum* Wall. as the valid name for this species, BEAN (1970) rejected this name, because most of the type material (Wallich 1225) represents *A. acuminatum*.

Both other series are monotypic. The species show some resemblance in their morphology as was already pointed out by WARSOW in 1903, but in other features they are rather distinct. *A. nipponicum* (series *Parviflora*) showed some affinities to *A. rufinerve* of series *Tegmentosa* (MOMOTANI, 1962), but heteroplastic grafting failed (see 6.6.3 and 6.6.5).

VI. **Section Trifoliata** Pax, in Engler, Bot. Jahrb., 6: 326 (1885) partly (excl. *A. cissifolium* Sieb. & Zucc.); ibid. in Engler Bot. Jahrb., 7: 203 (1886) partly (excl. *A. cissifolium*); ibid., in Engler, Pflanzenreich, IV, 163: 29 (1902) partly (excl. *A. cissifolium* and *A. henryi* Pax).

Lectotype species: *A. maximowiczianum* Miq. (fide Murray).

Heterotypic synonym: *Coelocarpa* Pax, l.c. 328 (1885). Type species: *A. mandshuricum* Maxim.

Trees or shrubs, bark sometimes exfoliating. *Leaves* trifoliolate, chartaceous, margins subentire to coarsely serrate. *Bud scales* 11–15-paired, grey-brown.

Inflorescences mostly 3-flowered, sometimes to 25 flowers (*A. sutchuenense*), racemose, sometimes corymbose (types III and II respectively), terminal and axillary. *Flowers* 5(–6)-merous; perianth green-yellow; stamens 10–13; disc extrastaminal, sometimes amphistaminal. *Fruits*: nutlets big, spherically convex; pericarp thick, lignified; parthenocarpic tendency strong. *Seedlings*: cotyledons narrowly ovate.

Area: C. China to N.E. Asia.

Species: *A. maximowiczianum* Miq., *A. shensiense* Fang & Hu (= preceding?), *A. griseum* (Pax) Franch., *A. triflorum* Komarov, *A. leiopodum* (Handel-Mazzetti) Fang & Chow (= preceding?), *A. mandshuricum* Maxim., *A. kansuense* Fang & Fang f. (= preceding?), *A. sutchuenense* Franch., *A. tienchuanense* Fang & Soong (= preceding?).

NOTES. POJARKOVA (1933) distinguished two series, *Grisea* and *Mandshurica*, which were accepted by FANG (1966) and MURRAY (1970). Because of their similarity these series were not accepted here. Most characteristic are the fruits in the latter series. The samaras has besides the cavities, which contains the embryos, a cavity between both nutlets.

MURRAY (1969) reported on the invalidity of the name *A. nikoense*, but gave only few details of this complicated question. In 1865 MIQUEL published *Negundo? nikoense* based on two leaves sent by KEISKE from Japan. These leaves should represent a trifoliolate maple of Mt. Nikko, but actually they belonged to *Parthenocissus tricuspidata* (S. & Z.) Planchon. This determination was made by HARA (unpublished?) at Leyden in 1966. In 1867 MAXIMOWICZ used the name *nikoense* to describe a trifoliolate maple of Japan and refered to MIQUEL's plant: '*Negundo? nikoënse* Miq. l.c. II 90. (specimini sterili superstructum)'. On the type specimen of the latter there is a note by MAXIMOWICZ himself, indicating affinities of these leaves with those of *A. cissifolium*. In 1880 he placed *Negundo? nikoense* in the synonymy of *A. cissifolium* and added to the name *A. nikoense*: 'Maxim. l.c. 370; nec Miq.' The oldest valid name, *A. maximowiczianum* Miquel (November 1867) was based on specimens of MAXIMOWICZ' collection.

VII. **Section Rubra** Pax, in Engler, Bot. Jahrb., 6: 326 (1885); ibid., in Engler, Bot. Jahrb., 7: 178 (1886); ibid., in Engler., Pflanzenreich, IV, 163: 37 (1902).

Type species: *A. rubrum* L.

Homotypic synonyms: *Clinotrox* Rafinesque, New Flora of N. Amer., 1:47 (1836) as a genus. *Rufacer* Small, Manual of the Southeastern Flora: 825 (1933) as a genus.

Heterotypic synonyms: *Eriocarpa* Rafinesque, l.c. 47 as a subgenus. Type species: *A. saccharinum* L. Homotypic synonyms: *Sacchrosphendamnus* Nieuwland, Amer. Midl. Nat., 3: 183 (1914) as a genus. *Argentacer* Small. l.c.: 825 as a genus

Trees, deciduous, axillary buds accumulated on the generative shoots. *Leaves* 3–5-lobed, glaucous beneath, margins serrate. *Bud scales* 4–7-paired, red. *Inflorescences* fasciculate-unbellate, (type IV), mostly 5-flowered, axillary, from leafless buds. *Flowers* 5-merous, perianth red, sometimes green-red, petals and disc sometimes wanting and sepals connate. (*A. saccharinum* L.), stamens mostly 5, disc intrastaminal, anthesis before leaf development. *Fruits*: nutlets small, somewhat convex or big, obovoid, ripening during early summer, low parthenocarpic tendency, immediate germination of the seeds. *Seedlings*: cotyledons thick, fleshy, obovate, hypogeal or thin, narrowly obovate, epigeal.

Area: Eastern N. America, Japan.

Species: *A. rubrum* L., *A. saccharinum* L., *A. pycnanthum* Koch.

NOTES. Section *Rubra* is not further divided as originally proposed by POJARKOVA (1933). The taxa show a high degree of resemblance in morphological characters and mode of reproduction. The evolution to anemophily is most advanced in *A. saccharinum*. The flowers are apetalous and lack a honey disc although petals were sometimes observed (see 2.2.2). The biosystematic studies of HASLAM (1965) and FOWDEN and PRATT (1973) showed a difference between *A. rubrum* and *A. saccharinum*, which was mostly not found between species of other series and sections (see 6.6.2).

VIII. **Section** *Ginnala*, Nakai, Bot. Mag. Tokyo, 29: 25 (1915).
Type species: *A. ginnala* Maxim.

Heterotypic synonyms: *Spicata* series *Tatarici* Pax, in Engler, Bot. Jahrb., 7: 183 (1886). Type species: *A. tataricum* L. Homotypic synonym: *Trilobata* Pojarkova, Acta Inst. Bot. Acad. Sci. U.S.S.R. 1 : 324 (1933) partly (ecxl. *A. isolobum* sensu Kurz), *A. paxii* Franch., *A. pilosum* Maxim., *A. trifidum* sensu Hooker & Arnoth (= *A. buergerianum* Miq.).

Shrubs, or small trees, deciduous. *Leaves* undivided or 3-lobed, chartaceous; margins serrate. *Bud scales* 5–10-paired, grey-brown. *Inflorescences* corymbose (type II), terminal and axillary, bracts distinct. *Flowers* 5-merous; perianth greenish white, somewhat rolled inwards during anthesis; stamens 8; disc extrastaminal; anthesis some time after the unfolding of the leaves. *Fruits*: nutlets rather flat, elliptic, strongly veined. *Seedlings*: cotyledons small, elliptic.

Area: C. and S.E. Europe, C. and N.E. Asia.

Species: *A. tataricum* L., *A. semenovii* Regel & Herder, *A. ginnala* Maxim., *A. aidzuense* (Franch.) Nakai (= preceding?), *A. theiferum* Fang (= preceding?).

NOTES. A small section with closely related taxa. Morphologically the species distinguished mainly vary in the lobation of the leaves. *A. aidzuense* is often considered as a *A. ginnala* variety. MOMOTANI (1961) studies showed a degree of difference, between these taxa (see 6.6.3).

IX. **Section Lithocarpa** Pax, in Engler, Bot. Jahrb. 6: 328 (1885), no species cited; ibid., in Engler, Bot. Jahrb. 7:249 (1886), partly (excl. *A. argutum* Maxim., *A. barbinerve* Maxim.); ibid., in Engler, Pflanzenreich, IV, 163: 70 (1902), partly (excl. besides species listed above: *A. tetramerum* Pax (= *A. stachyophyllum* Hiern)).

Lectotype species: *A. villosum* sensu Wallich (= *A. sterculiaceum* Wall.) (fide Murray).

Homotypic synonym: *Sterculiacea* Murray, Kalmia, 1: 41 (1969) partly (excl. *A. pilosum* Maxim.) as subgenus.

Heterotypic synonyms: *Diabolica* Koidzumi, Journ. Coll. Sci. Univ. Tokyo, 32, 1: 64 (1911). Type species: *A. diabolicum* Koch.

Sphendamus Rafinesque, New Flora of N. Amer., 1: 48 (1836) as subgenus. Type species: *A. macrophyllum* Pursh. Homotypic synonym: *Macrophylla* (Pojarkova) Momotani, Mem. Coll. Sci. Kyoto B, 29: 184 (1962). Basionym: *Platanoidea* series *Macrophylla* Pojarkova, Acta Inst. Acad. Sci. U.S.S.R., 1, 1: 326 (1933).

Trees, big, deciduous, branches rather thick. *Leaves* big, 3–5-lobed, sometimes subentire, chartaceous, margins lobulate or entire, sometimes serrate. *Bud scales* 5–8- or 8–12-paired. *Inflorescences* racemose or corymbose, rachis elongated. *Flowers* large, 5-(6-)merous, perianth green-yellow, stamens 8–12, disc amphistaminal. *Fruits*: nutlets keeled convex, mostly covered with stiff hairs, pathenocarpic tendency strong. *Seedlings*: cotyledons narrowly oblong, obtuse.

The section includes two series:

A. **Series Lithocarpa.**

Type species: *A. sterculiaceum* Wall.

Homotypic synonym: *Villosa* Pojarkova, l.c.: 236, nomen nudum.

Heterotypic synonym: *Diabolica* (Koidzumi) Momotani, l.c.: 187. Basionym: *Diabolica* Koidzumi, l.c. as section. Type species: *A. diabolicum* Koch.

Trees, dioecious. *Leaves* 3–5-lobed, sometimes subentire; margins remotely dentate to serrulate, sometimes entire; petioles sometimes lactiferous *Bud scales* 8–12-paired, grey-brown. *Inflorescences* racemose, sometimes partly corymbose (type III and II respectively), axillary from leafless buds, 10–20 flowers *Flowers* 5-merous; perianth sometimes connate (♂ specimens of *A. diabolicum* and *A. sinopurpurascens*); mostly 8-stamened.

Area: Himalaya, C. and E. China, Japan.

Species: *A. sterculiaceum* Wall., *A. francheti* Pax (= preceding?), *A. thomsonii* Miq. (= preceding?), *A. huianum* Fang & Hsien (= preceding?), *A. lungshengense* Fang & Hu (= preceding?), *A. tsinglingense* Fang (= preceding?), *A. kungshanense* Fang & Chang (= preceding?), *A. leipoënse* Fang & Soong, *A. diabolicum* Koch, *A. sinopurpurascens* Cheng.

B. **Series Macrophylla** Pojarkova, l.c.: 236.
Type species: *A. macrophyllum* Pursh.
Homotypic synonym: *Sphendamus* Rafinesque, l.c. as subgenus.

Trees, monoecious. *Leaves* deeply 5-lobed; margins lobulate to entire; petioles lactiferous. *Bud scales* 5–8-paired, green-red. *Inflorescences* big, corymbose, (type II), 30–80 flowers, terminal and axillary. *Flowers* 5–6-merous.
Monotypic: *A. macrophyllum* Pursh, western N. America.

Notes. In its present delimitation section *Lithocarpa* was first recognized by Pojarkova (1933). It includes two somewhat remotely related series with distinct geografic areas and with resemblances in their reproductive organs. Series *Lithocarpa* includes the most specialised taxa. They are dioecious and develop their inflorescences from leafless lateral buds. Part of the taxa have lactiferous petioles, e.g. *A. sinopurpurascens.* Murray (1969), who proposed a separate subgenus, *Sterculiacea,* for these taxa, distinguished a large complex species *A. sterculiaceum.* Ogata (1967) considered one of the species, which Murray made conspecific, namely *A. thomsonii,* as somewhat apart phylogenetically from the other species, rather than *A. diabolicum,* of which the ♂ flowers have a connate perianth. Fang (1966) described 5 new species, of which only a specimen of *A. leipoënse* could be studied. It was found to be distinct and not synonymous with *A. sterculiaceum* subsp. *franchetii* as suggested by Murray (1970). Further revision of this series is needed.

Although series *Macrophylla* has two main characters the lactiferous petioles and the amphistaminal disc, in common with series *Platanoidea,* several other features indicate affinities to series *Lithocarpa.*

X. **Section Negundo** (Boehmer) Maximowicz, Bull. Acad. Sci. St. Petersb., 26: 450 (1880), partly (excl. *A. nikoense* Maxim. non Miquel (= *A. maximowiczianum* Miq.), *A. mandshuricum* Maxim., and *A. discolor* Maxim.).
Type species: *A. negundo* L.
Basionym: *Negundo* Boehmer, in Ludwig, Def. Gen. Plant., ed. 3:508 (1760) as genus. Homotypic synonyms: *Rulac* Adanson, Fam. Nat. des Plantes, 2: 383 (1763), nomen nudum. *Negundium* Rafinesque, Atlantic Journ., 6: 176 (1833) as genus.
Heterotypic synonym: *Cissifolia* Koidzumi, Journ. Coll. Sci. Univ. Tokyo, 32, 1: 26 (1911). Type species: *A. cissifolium* (Sieb. & Zucc.) K. Koch.

Trees or shrubs, deciduous, dioecious. *Leaves* chartaceous, compound, trifolioate or pinnate, 5–7 foliolate, margins of leaflets entire to remotely dentate. *Bud scales* 2–3-paired. *Inflorescences* racemose or compound racemose (type III and V respectively), axillary from leafless buds or accompanied of 1–2-pair of small leaves, which drop precociously, 15–50 flowers. *Flowers* 4-merous; stamens 4–6, absent in ♀ flowers. *Fruits*: nutlets small elliptic-spherical to rather flat, veined, parthenocarpic tendency strong. *Seedlings*: cotyledons, narrowly oblong.

The section includes two series:

A. **Series Negundo**

Leaves pinnate, 3–7, sometimes to 9-foliate. *Bud scales* 2-, more often 3-paired. *Inflorescences* racemose (♀ individuals) or compound racemose (♂); long drooping pedicels. *Flowers* apetalous; greenish; disc wanting; anemophilous; anthesis before leaf development.

Monotypic: *A, negundo* L., N. America to Guatemala.

B. **Series Cissifolia** (Koidzumi) Pojarkova, Acta Inst. Bot. Acad. Sci. U.S.S.R., 1: 240 (1933).

Type species: *A. cissifolium* (Sieb. & Zucc.) Koch.

Basionym: *Cissifolia* Koidzumi, l.c.: 26 as section.

Leaves trifoliolate. *Bud scales* 2-paired, *Inflorescences* racemose, rachis long, 15–30 flowers. Flowers 4-merous; sepals and petals very distinct, greenish-white or yellow; stamens 4–6; disc amphistaminal; entomophilous; anthesis during leaf-development.

Area: Japan, S.W. China.

Species: *A. cissifolium* Sieb. & Zucc., *A. henryi* Pax.

NOTES. Section *Negundo* includes two highly specialised series, both dioecious. The close relationship of both series was recognized by MOMOTANI (1962) and MURRAY (1970), who included both series (as sections) in a subgenus *Negundo*. Biosystematic studies also showed the affinities of both series (see 6.6.2; 6.6.4; 6.6.5).

MURRAY (1966) combined *A. cissifolium* from Japan and *A. henryi* from C. China. Both species agree in most morphological characters, but vary in the corolla of the flowers. *A. cissifolium* has long, narrow, yellow petals, while *A. henryi* has rather small whitish petals, which mostly drop before or during anthesis. Although both species were successfully crossed, spontaneous hybridization in collections may rather rarely occur. The present author does not accept them as conspecific.

XI. **Section Glabra** Pax, in Engler, Bot., Jahrb., 6: 327 (1885); ibid., in Engler, Bot. Jahrb., 7: 217 (1886); ibid., in Engler, Pflanzenreich, IV, 163: 45 (1902).

Type species: *A. glabrum* Torrey.

Heterotypic synonym: *Arguta* Rehder, in Sargent, Trees and Shrubs, 1: 181 (1905). Type species: *A. argutum* Maxim.

Trees and shrubs, deciduous. *Leaves* chartaceous, undivided, 3–5-lobate, sometimes (partly) trifoliolate, margins serrate. *Bud scales* 2–4-paired. *Inflorescences* small, racemose or corymbose (type III and II respectively), terminal and, sometimes exclusively, axillary, 10–25 flowers. *Flowers* 4- or 5-merous, yellowish; disc amphi- to intrastaminal. *Fruits*: nutlets flat, glabrous, strongly veined, parthenocarpic tendency strong. *Seedlings*: cotyledons small, obovate.

The section includes two series:

A. **Series Glabra**

Shrubs or small trees. *Leaves* 3-lobed, sometimes 5-lobed or (partly) trifoliolate. *Bud scales* 2–4-paired. *Inflorescences* corymbose or racemose, terminal and axillary. *Flowers* 5-merous; stamens 8; disc amphi- to intrastaminal.

Monotypic: *A. glabrum* Torrey, western N. America.

B. **Series Arguta** (Rehder) Pojarkova, Acta Inst. Bot. Acad. Sci. U.S.S.R., 1: 240 (1933).

Basionym: *Arguta* Rehder, l.c., as section.

Type species: A. *argutum* Maxim.

Trees and shrubs, dioecious. *Leaves* undivided or 3–5-lobed. *Inflorescences* of ♂ individuals axillary from leafless buds, of ♀ individuals terminal and axillary from mixed buds. *Flowers* 4-merous; stamens 4(–6), mostly wanting in ♀ flowers; disc amphi- to intrastaminal.

Area: Himalaya to N.E. Asia.

Species: *A. argutum* Maxim., *A. barbinerve* Maxim., *A. acuminatum* Wallich ex D. Don, *A. stachyophyllum* Hiern (syn. *A. tetramerum* Pax), *A. muliense* Fang & Hu (preceding?).

NOTES. MOMOTANI (1962) proposed section *Glabra* as it is accepted here. POJARKOVA (1933) first recognized the affinities of both series. The taxa of both series strongly resemble in most morphological characters. Series *Arguta* includes a natural group of dioecious species. *A. stachyophyllum* is a large variable species of which several taxa are better known as *A. tetramerum* Pax. MURRAY (1970) correctly placed this name in the synonymy of the former species.

XII. **Section Integrifolia** Pax, in Engler, Bot. Jahrb., 6, 327 (1885) no species cited; ibid., in Engler, Bot. Jahrb., 7, 207 (1886) partly (excl. *A. niveum* Blume (= *A. laurinum* Hasskarl)), *A. laevigatum* Wall., *A. reticulatum* Champ., *A. fabri* Hance); ibid., in Engler, Pflanzenreich, IV, 163: 31 (1902) partly (excl. *A. niveum* Blume, *A. laevigatum* Wall., *A. cordatum* Pax, *A. schwerinii* Pax, *A. discolor* Maxim.). Maxim.).

Lectotype species: *A. oblongum* Wall. ex DC. (fide Murray).

Homotypic synonyms: *Integrifolia* series *Trinervium* Metcalf, Lingnan Sci. Journ., 11: 202 (1932), partly (excl. *A. laevigatum* Wall.). *Integrifolia* series *Oblonga* Pojarkova, Acta Inst. Bot. Acad. Sci. U.S.S.R., 1, 1: 238 (1933), nomen nudum. *Integrifolia* subsection *Oblongae* Hy & Cheng, Bull. Fan Mem. Inst. Biol. Peiping, 1, 200 (1948).

Heterotypic synonyms: *Pentaphylla* Hu & Cheng, l.c.: 208. Type species: *A. pentaphyllum* Diels.

Spicata series *Trifidi* Pax, in Engler, Bot. Jahrb., 7: 183 (1886) partly (excl. *A. pilosum* Maxim., *A. cinerascens* Boiss. (= *A. monspessulanum* L.)). Type species: *A. trifidum* Hook & Arnot (= *A. buergerianum* Miq.). Homotypic synonyms: *Trilobata* Pojarkova series *Trifida* Pojar., l.c., partly (excl. *A. pilosum* Maxim., *A. isolobum* Kurz.). *Microcarpa* series *Buergeriana* Fang, Acta Phytotax. Sinica, 11, 162 (1966), partly (excl. *A. pilosum* Maxim., *A. taipuense* Fang, *A. fenzelianum* Handel-Mazzetti, *A. tonkinense* Lecomte, *A. liquidambarifolium* Hu & Cheng (= preceding), *A. calcaratum* Gagnep., *A. chapaense* Gagnep., *A. isolobum* Kurz (= *A. osmastonii* Gamble)).

Trees, mostly evergreen. *Leaves* undivided or 3-lobed, sometimes compound, 5–7-palmatifoliolate, usually glaucous beneath, margins entire to lobulate-serrate. *Bud scales* 4-8-paired, grey-brown. *Inflorescences* corymbose (type II), bracts distinct, terminal and axillary, 25–75 flowers. *Flowers* 5-merous, perianth yellow-white, petals longer than sepals, stamens mostly 8, disc extrastaminal. *Fruits*: nutlets keeled convex, parthenocarpic tendency strong. *Seedlings*: cotyledons small, narrowly oblong, acuminate.

The section includes two series:

A. **Series Trifida** Pax, l.c., partly, as *Trifidi.*

Type species: *A. buergerianum* Miq.

Homotypic synonyms: *Trifida* Pojarkova, l.c., partly. *Buergeriana* Fang, l.c., partly.

Heterotypic synonyms: *Trinervium* Metcalf, l.c., partly. Lectotype species: *A. oblongum* Wall. ex DC. (fide Murray).

Leaves mostly persistent, undivided or 3-lobate, margins entire to lobulate-serrate.

Area: Himalaya to C. and S.E. China, Taiwan.

Species: *A. oblongum* Wall. ex DC., *A. lanceolatum* Molliard (= preceding?), *A. albopurpurascens* Hayata (= preceding?), *A. laikuanii* Ling (= preceding?), *A. paxii* Franch., *A. hilaense* Hu & Cheng (= preceding?), *A. kwangnanense* Hu & Cheng (= preceding?), *A. coriaceifolium* Léveillé, *A. buergerianum* Miq., *A. lingii* Fang (= preceding?), *A. yuii* Fang, *A. wangchii* Fang, *A. sycopsoides* Chun.

B. **Series Pentaphylla** (Hu & Cheng) Murray, Kalmia, 2: 1 (1970).

Basionym: *Pentaphylla* Hu & Cheng, l.c. as section.

Type species: *A. pentaphyllum* Diels.

Leaves compound, 5-, sometimes to 7-palmatifoliolate, margins serrate to entire.

Monotypic: *A. pentaphyllum* Diels, S. W. China.

NOTES. Series *Pentaphylla* is included in this section because of the strong resemblances of the branches, bud scales, inflorescences and fruits with those of series *Trifida*. The flowers of the single species in series *Pentaphylla*, *A. pentaphyllum*, could not be studied, but according to HU and CHENG's (1948) description they may resemble those of series *Trifida*. The taxa of series *Trifida* form a rather natural group, but a large number of them, especially those described from S. China, are very little known.

The Stryberg Arboretum, Los Angelos, USA, contains some trees from seeds collected from the tree of which J. Rock gathered the type material of *A. pentaphyllum*. All other plants in cultivation in the USA and W. Europe are grown from scions of the Stryberg Arboretum specimens.

XIII. **Section Indivisa** Pax, in Engler, Bot. Jahrb., 6: 327 (1885) no species cited; ibid., in Engler, Bot. Jahrb., 7:213 (1886) partly (excl. *A. stachyophyllum* Hiern., *A. sikkimense* Miq., *A. hookeri* Miq., *A. davidii* Franch., *A. distylum* Sieb. & Zucc., *A. thomsonii* Miq.); ibid., in Engler, Pflanzenreich, IV, 163: 33 (1902) partly (excl. besides species cited above: *A. laxiflorum* Pax, *A. crataegifolium* Sieb. & Zucc., *A. veitchii* Schwerin (= preceding)).

Lectotype species: *A. carpinifolium* Sieb. & Zucc. (fide Murray).

Homotypic synonym: *Carpinifolia* Koidzumi, Journ. Coll. Sci. Univ. Tokyo, 32 : 17 (1911).

Small trees or shrubs, deciduous, terminal buds usually aborted, dioecious. *Leaves* undivided, nerves unicostate, lateral veins parallel as in *Carpinus*, margins double serrate. *Bud scales* 9–13-paired, brown. *Inflorescences* racemose (type III) terminal and axillary from mixed buds, 10–20 flowers. *Flowers* 4-merous; perianth greenish-yellow; ♂ flowers often apetalous; stamens mostly 6; disc amphistaminal-intrastaminal. *Fruits*: nutlets narrowly elliptic-spherical to rather flat, glabrous; parthenocarpic tendency strong. *Seedlings*: cotyledons narrowly oblong, acuminate.

Monotypic: *A. carpinifolium* Sieb. & Zucc., Japan.

XIV. **Section Hyptiocarpa** Fang, Acta Phytotax. Sinica, 11: 172 (1966).

Type species: *A. decandrum* Merrill (= *A. garrettii* Craib).

Homotypic synonyms: *Decandra* (Hu & Cheng) Ogata, Bull. Tokyo Univ. For., 63: 153 (1967). Basionym: *Integrifolia* Pax subsection *Decandrae* Hu & Cheng, Bull. Fan Mem. Inst. Biol. Peiping, 1: 206 (1948). *Hyptiocarpa* Fang series *Decandra* (Hu & Cheng) Fang, l.c.: 173.

Heterotypic synonyms: *Laurina* Ogata, l.c.: 151. Type species: *A. laurinum* Hasskarl.

Hyptiocarpa series *Machilfolia* Fang, l.c.: 173. Type species: *A. machilifolium* Hu & Cheng.

Trees, evergreen, sometimes deciduous. *Leaves* undivided, coriaceous, glaucous beneath, margins entire. *Bud scales* 7–11-paired. *Inflorescences* corymbose or racemose (type II and III respectively), axillary from leafless buds. *Flowers*

5-merous, perianth yellowish, stamens 4-6, 8 or 8–12, disc mostly amphistaminal, sometimes nearly extra- or intrastaminal. *Fruits*: nutlets, big, obovoid; parthenocarpic tendency very weak (aborted seedless mericarp). *Seedlings* not seen.

Area: Subtropic mountains of S.E. Asia: Birma, Laos, N. Vietnam, S. China, Malaya, Philippine Islands, Indonesia (e.g. Java, Borneo, Celebes).

Species: *A. garrettii*, Craib (syn. *A. decandrum* Merrill), *A. longicarpum* Hu & Cheng (= preceding?), *A pinnatinervium* Merrill (= preceding?), *A. laurinum* Hasskarl, *A. philippinum* Merrill (= preceding?), *A. curannii* Merrill (= preceding?), *A. machilifolium* Hu & Cheng.

NOTES. The taxa of section *Hyptiocarpa* are very little known. This may be illustrated by FANG (1966), who recognized two series in this section, while he placed *A. garrettii* and *A. laurinum* in section *Integrifolia*, by OGATA (1967), who recognized two sections, and MURRAY (1970), who combined most of the taxa in one species.

A variable character is the number of stamens. It was found that within the area the more northern taxa have (8–)12 stamens, while the southern have (4–)5(–8) stamens.

The type specimen of *A. garrettii* CRAIB (1920) from N.E. Birma appeared to be very similar to specimens of Laos, N. Vietnam and S. China. From the latter area MERRILL (1932) described *A. decandrum*, which in the opinion of the present author is a synonym of *A. garrettii*. Both have persistent leaves, rather small racemose inflorescences, flowers with a somewhat hairy disc and 8–12 stamens.

A. laurinum from Indonesia strongly varies from the former. The trees are deciduous and the flowers appear, when the trees are bare. The inflorescences are larger and mostly corymbose, the flowers mostly have 5 stamens and a glabrous disc.

6.5. KEY TO THE SECTIONS AND SERIES

1. Leaves simple 6
   Leaves compound 2
2. Leaves trifoliolate or pinnate 3
   Leaves palmatifoliolate, 5(–7) leaflets . . . . Series **Pentaphylla**
3. Bud scales 2–4-paired 4
   Bud scales 11–15-paired . . . . Section **Trifoliata**
4. Inflorescences terminal and axillary: flowers 5-merous, stamens 8 . . . . Series **Glabra**
   Inflorescences axillary; flowers 4-merous, stamens 4–6; dioecious . . . . Section **Negundo** 5
5. Leaves trifoliolate; flowers with petals and honey disc. Asia . . . . Series **Cissifolia**
   Leaves pinnate, 3–7 leaflets; flowers apetalous, honey disc wanting. N. America . . . . Series **Negundo**

6\. Bud scales 2–4-paired 7

Bud scales 5- or more paired 16

7\. Bud scales always 2-paired, valvate 10

Bud scales 2–4-paired 14

Bud scales always 4-paired, terminal buds usually wanting . . . . Section **Palmata** 8

8\. Leaves undivided, coriaceous, persistent . . . . . . Series **Penninervia**

Leaves 3–13-lobed 9

9\. Leaves 3–7-lobed; inflorescences mostly large and erect, pedicels of blown ♂ flowers partly dropped; nutlets mostly without veins, pericarp thin. Subtropical areas . . . . Series **Sinensia**

Leaves 5–13-lobed, suborbiculair; inflorescences rather small, peduncle mostly drooping, pedicels of blown ♂ flowers completely dropped; nutlets mostly veined. Temperate areas . . . . Series **Palmata**

10\. Inflorescences racemes or small corymbs, the latter with the secondary axes opposite and large bracts, 10–25 flowers . Section **Macrantha** 11

Inflorescences large corymbs with cincinni, 20–400 flowers . . . . Section **Parviflora** 12

11\. Shoots striped, axillary buds stalked; inflorescences racemose . . . . Series **Tegmentosa**

Shoots with stiff hairs; inflorescences with distinct bracts and opposite secondary axes . . . . Series **Wardiana**

12\. Leaves undivided; inflorescences erect; nutlets veined. Japan . . . . Series **Distyla**

Leaves 3–5(–7)-lobed 13

13\. Leaves three-lobed, large; inflorescences large, peduncle drooping; nutlets globose. Japan. Series **Parviflora**

Leaves 3–5(–7)-lobed; inflorescences erect, pedicels of blown ♂ flowers partly dropped; nutlets small, rather flat . . . . Series **Ukurunduensia**

14\. Inflorescences large, erect, with small cincinni; flowers with narrow petals, twice as long as the sepals; nutlets small, not strongly veined; parthenocarpic tendency low to moderate . . . . Series **Ukurunduensia**

Inflorescences small, racemose or corymbose; petals as long as the sepals; nutlets strongly veined, parthenocarpic tendency strong . . . . Section **Glabra** 15

15\. Inflorescences terminal and axillary from mixed buds; flowers 5-merous, stamens 8. Western N. America . . . . Series **Glabra**

Dioecious; ♂ inflorescences axillary from leafless buds, ♀ inflorescences terminal and axillary from mixed buds; flowers 4-merous, stamens 4–6, East Asia.. . . . . Series **Arguta**

16\. Inflorescences terminal and axillary from mixed buds 19

Inflorescences axillary from leafless buds. 17

17\. Leaves undivided, coriaceous. . . . . Section **Hyptiocarpa**

Leaves lobed, chartaceous 18

18. Bud scales 4–7-paired; inflorescences in clusters, fasciculate-umbellate; flowers perianth red or green-red, stamens 5; . . . . . . Section **Rubra**
Bud scales 8–12-paired; inflorescences racemose; flowers: perianth yellow-green, stamens 8–12; . . . . Series **Lithocarpa**
19. Leaf petioles lactiferous; honey disc amphistaminal, stamens 8–12. . 20
Leaf petioles not lactiferous; honey disc extrastaminal, stamens 8, or amphistaminal, stamens 5 21
20. Inflorescences with drooping peduncle, rachis long; stamens 8–12; nutlets keeled convex. Western N. America . . . . Series **Macrophylla**
Inflorescences erect; stamens 8; nutlets flat; Europe, Asia . . . . Series **Platanoidea**
21. Leaves undivided, biserrate, chartaceous; inflorescences racemose; dioecious; nutlets flat . . . . Section **Indivisa**
Inflorescences corymbose; monoecious (sometimes ♂ specimens); . . 22
22. Leaf margins entire to coarsely serrate; nutlets spherically convex and often keeled, or flat 23
Leaf margins biserrate; nutlets elliptically convex, veined . . . . Section **Ginnala**
23. Flower stamens 8, disc extrastaminal; nutlets convex, often keeled. . 24
Flower stamens 5, disc amphistaminal; nutlets flat . . Series **Pubescentia**
24. Leaves undivided to 3-lobed, usually coriaceous, persistent; flowers whitish-yellow, petals narrow, longer than sepals, stamens not well-excerted, strong parthenocarpic tendency . . . . Series **Trifida**
Leaves 3–7-lobed, rarely unlobed, chartaceous, sometimes coriaceous and persistent; flowers green-yellow, petals rather broad, as long as sepals, stamens well-excerted, fruits: parthenocarpic tendency strong to moderate . . . . Section **Acer** 25
25. Flowers apetalous, calyx connate, long drooping pedicels. Eastern N. America . . . . Series **Saccharodendron**
Flowers with corolla, calyx not connate . . . .
26. Leaves big, 5–7-lobed, chartaceous, inflorescences big; flowers with rather short pedicels; fruits: parthenocarpic tendency moderate . . Series **Acer**
Leaves variable, 3–5-lobed, chartaceous, sometimes coriaceous and persistent; inflorescences moderate to small; flowers with long drooping pedicels, somewhat shorter on evergreen specimens; fruits: parthenocarpic tendency strong . . . . Series **Monspessulana**

6.6. SURVEY OF BIOSYSTEMATIC STUDIES

6.6.1. *Anatomy*

OGATA (1967) studied the wood anatomy of a large number of species, representing the major part of the sections distinguished. He found that taxa, which morphologically showed relationships, also had rays of similar width and shape. Such a resemblance was for example noticed in section *Acer* with representatives of the 3 series distinguished by the present author (see 6.5).

The examined specimens of the monotypic section *Indivisa* had very big rays, deviating from other taxa of the genus, but generally the anatomical wood characters showed a strong resemblance throughout the genus. The amount and distribution of crystals in the stem wood were fairly characteristic in each section, but large variations were noticed in the sections *Acer* and *Palmata.*

WATARI (1936) and COURTESI (1943) studied the vascular system in the leaf petioles. The former examined about 30 species, mainly those endemic to Japan and Taiwan. He observed two manners in which the ventral bundle could be formed, indicated as M-type and M-L-type. The first condition usually occurred in the section *Palmata* (except *A. oliverianum*) and series *Tegmentosa* (except *A. crataegifolium*). The species mainly had petioles with a bifacial structure over the entire length. An unifacial structure was found in the sections *Acer* (*A. pseudoplatanus*), *Palmata* and *Platanoidea* (except *A. campestre* and *A. miyabei*).

CORTESI (1942) studied very poorly identified herbarium specimens. His results have no further taxonomic importance.

POWERS (1967) made a blade tissue study of 45 species and varieties of *Acer* and *Dipteronia.* The short article, based on his thesis, does not contain taxonomic considerations.

6.6.2. *Chemistry*

MOMOTANI (1961, 1962) analysed the seed proteins of 43 *Acer* species by means of turbidometric titration. He could clearly demonstrate affinities between related taxa, but his diagram of affinities for the whole genus does not represent a phylogenetic scheme. His results pointed to strong affinities of *A. campestre* from Europe and *A. miyabei,* which occurs in Japan, *A. rufinerve* (Series *Tegmentosa*) and *A. nipponicum* (series *Parviflora*), *A. glabrum* (series *Glabra*) and the species of series *Arguta, A. opalus* (series *Monspessulana*) and *A. heldreichii* and *A. trautvetteri* (series *Acer*). Some species with very strong affinities were e.g. *A. heldreichii* and *A. trautvetteri, A. spicatum* and *A. ukurunduense, A. ginnala* and *A. tataricum, A. griseum* and *A. maximowiczianum, A. barbinerve* and *A. stachyophyllum.* Some morphologically closely related taxa, which were not confirmed in the tests were *A. ginnala* and *A. aidzuense* (often considered as *A. ginnala* variety) and the *A. palmatum* subsp. *amoenum, matsumurae* and *palmatum.*

ZIEGENFUS and CLARKSON (1971) made a comparison of the soluble seed proteins of 7 taxa of *Acer* native to eastern N. America. They found close protein similarities of the 3 subspecies of *A. saccharum* studied: *floridanum, nigrum* and *saccharum.* A relative high protein similarity of *A. rubrum* and *A. saccharinum* was noticed. *A. negundo* was found to have relatively high protein resemblance to the *A. saccharum* subspecies. *A. rubrum* and *A. spicatum* were shown to have the least protein similarity to the other taxa investigated.

TOWERS and GIBBS (1953), studying the syrangaldehyde/vanillin (s/v) values in 17 *Acer* and 2 *Dipteronia* species, found rather low values in *A. cissifolium* (0.5), *A. henryi* (0.6), *A. negundo* (0.5), *Dipteronia dyerana* (1.0) and *D. sinensis* (0.3). The mean value for the remaining *Acer* species was (2.0). The results of the 'Maüle'-tests, in which 29 *Acer* species were studied, roughly corresponded with the s/v values found. Section *Negundo* showed a very weak hydrochloric acid/methanol reaction.

RIOU and DELORNE (citate TOWERS and GIBBS) found that *A. negundo* strikingly varied in manganese content from the other 5 species of eastern N. America.

HASLAM (1965) studied paper chromatographically gallyol esters in the leaves of 14 *Acer* species. On the basis of the occurrence of these esters he could distinguish 3 groups. Group A consisted of *A. ginnala, A. tataricum* and *A. saccharinum*, group B included *A. campestre, A. platanoides* and *A. rubrum*, and group C the remaining species: *A. griseum, A. monspessulanum, A. opalus, A. palmatum, A. pensylvanicum, A. pseudoplatanus, A. saccharum* and *A. spicatum*. *A. macrophyllum* only produced free gallic acid, which was found in a higher concentration than in the other species studied.

HEINE (1966) studied the occurrence of saponins in leaves and barks of 19 species. Saponins were found in the representatives of the sections *Ginnala, Indivisa* and *Rubra* and the series *Acer, Negundo* and *Platanoidea*, while they were absent in the section *Trifoliata* and the series *Arguta, Monspessulana, Palmata* and *Saccharodendron*.

FOWDEN and PRATT (1973) studied the distribution and biosynthesis of cyclopropylamino acids in the seeds of 22 species. Of the 4 compounds studied, 3 were previously discribed for members of the *Sapindaceae* and *Hippocastanaceae*, while the fourth was also found in *Billia hippocastanum* (*Hippocastanaceae*). All compounds were found in the studied specimens of series *Acer, Distyla, Macrophylla, Negundo, Saccharodendron* and *Ukurunduensia* and in *A. saccharinum* (section *Rubra*). The studied specimens of series *Palmata* mostly had only two of the four compounds, while no compounds were found in the sections *Ginnala* and *Trifoliata*, the series *Glabra, Platanoidea*, and *Tegmentosa* and in *A. rubrum* (section *Rubra*).

6.6.3. *Karyology*

Reports on chromosome numbers were published by e.g. TAYLOR (1920, FOSTER (1933), WRIGHT (1957), MEHRA c.s. (1972) and SANTAMOUR (1971). The basic number (2n = 26) was found in most of the species studied. *A. carpinifolium, A. pseudoplatanus* and *A. saccharinum* were reported to be tetraploid (2n = 52). *A. pycnanthum* was found to be hexaploid (2n = 78; SANTAMOUR, 1971).

Various numbers were counted in the case of *A. rubrum*: 78, 104 (DUFFIELD, 1940, 1943; SANTAMOUR, 1965), 91 (SANTAMOUR, 1965), c. 72, c. 108, c. 144 (TAYLOR, 1920), 65, 78, (ELLIS, 1964). These all concern diploid numbers.

6.6.4. *Genetics*

Species of the same series often spontaneously hybridize in collections (e.g.

series *Acer, Platanoidea, Saccharodendron, Tegmentosa*).

Data on successful and failed species crosses were provided by WRIGHT (1953). Successful combinations of species of different series or sections were: *A. campestre* with *A. monspessulanum, A. opalus* and *A. pseudoplatanus*; *A. monspessulanum* with *A. campestre, A. pseudoplatanus* and *A. tataricum*; *A. negundo* with *A. henryi, A. platanoides* and *A. saccharinum*; *A. platanoides* with *A. negundo* and *A. saccharum*; *A. tataricum* with *A. campestre, A. monspessulanum, A. negundo* and *A. pensylvanicum*; *A. rubrum* and *A. saccharinum* (both section *Rubra*).

6.6.5. *Heteroplastic grafting*

Heteroplastic grafting also gives information about affinities of various taxa of the genus. PITCHER (1960) grafted scions of several species on *A. saccharum* rootstocks. Although his results with *A. saccharum* scions were rather poor, he mentioned some successful combinations with *A. monspessulanum, A. platanoides* and *A. spicatum*.

By Mr. D. M. van Gelderen, Boskoop, Mr. W. J. M. Jansen, Curator of Wageningen Bot. Gardens and Mr. A. Peters, Opheusden I learned that *A. pseudoplatanus* and *A. rubrum* were successfully used as rootstocks for several other species. The former may be grafted with *A. grosseri, A. lobelli* (!) *A. pentaphyllum, A. rubrum, A. rufinerve* and *A. sinopurpurascens*, the latter with *A. griseum, A. pentaphyllum* and *A. triflorum*.

Within the same series combinations were mostly succesful: *A. palmatum* with *A. circinatum, A. japonicum, A. pseudosieboldianum, A. shirasawanum* a.o.; *A. platanoides* with *A. cappadocicum, A. lobelii* and *A. mono*; *A. campestre* with *A. divergens* and *A. miyabei*; *A. rufinerve* with *A. davidii, A. grosseri, A. tegmentosum* and others. *A. henryi* on *A. negundo* was successful in only 10% of the grafts, while *A. nipponicum* failed on *A. rufinerve*.

6.7. PALAEOTAXONOMY

The characteristic palmately lobed leaf and the winged fruit made *Acer* easily recognisable among plant fossils. This led to the description of numerous fossil species by, among others, Ettingshausen, Heer, Saporta and Unger in papers on the Tertiary floras of C. Europe, Greenland, Spitsbergen, N. America and Japan. In his monograph on the genus *Acer* PAX (1885, 1886) classified these species in sections in the same way as the living taxa and named these sections *Palaeopalmata, Palaeoplatanoidea, Palaeorubra*, etc.

The variability of the leaves and the somewhat superficial study of other morphological characters, such as bud scales, flowers and inflorescences, led to rather artificial classifications. Consequently the classification of fossil maples was often rather doubtful. Most authors understood these problems and made special remarks on the limitation of their studies.

New methods to study fossil leaves increased the possibilities of classification. The structures of the epidermis appeared to be very characteristic and useful to distinguish fossil species. A method for typographical cuticula analysis, developed by KRAUSEL and WEYLAND (1959), was succesfully used by HANTKE (1965) and WALTER (1972). The former could show that 14 described fossil species were synonymous with *A. tricuspidatum* Bronn. WALTER proved the occurrence in C. Europe, during the Tertiary, of representatives of the sections *Acer*, (inclusive series *Saccharodendron*) and *Rubra*, and the series *Palmata* and *Platanoidea*. The leaves of most of these maples show resemblances in their lobation, having three, large, oblong, acuminate lobes with remotely dentate to serrulate margins.

One species, *A. rueminianum* Heer sensu Hantke, could not be classified by WALTER in one of the present sections. He tentatively suggested an extinct section, but at the same time he pointed to his incomplete knowledge of the genus. The present author noticed much resemblance to leaves of *A. pilosum* of series *Pubescentia*.

7. EVOLUTION

7.1. INTRODUCTION

Biosystematics is in fact evolution biology. An understanding of the processes which have led to the segregation of the taxa is more important than the diversities themselves. In this final chapter the results of the studies of morphologic characters (chapter 2), of flowering and of sex expression (chapters 3, 4 and 5) and of taxonomy (chapter 6) will be discussed further to examine the evolutional trends in the genus.

The literature on the phylogeny of *Acer* is rather extensive. The large variability within the genus and many fossil records stimulated phylogenetic studies. Papers which concerning origin and migration, and the phylogeny of the whole genus are reviewed in the next paragraph, other papers dealing with evolutional trends of certain characters are mentioned in the paragraphs on the corresponding subjects.

The evolution of *Acer* can only be studied when related taxa, such as *Dipteronia*, *Hippocastanaceae* and *Sapindacea*, are also considered.

7.2. LITERATURE

CROIZAT (1952; quotation DESCHENES, 1970) stated that *Acer* originated in pre-Jurassic time where the Indian Ocean is now located. This mainly because of the relations of the *Aceraceae* with the *Sapindaceae*, which originated in the southern hemisphere. The *Aceraceae* followed two main tracks; one directed towards Malaysia and the other towards Iran. PAX (1926) and POJARKOVA (1933) indicated the present major centre, eastern Asia, and especially the mountainous areas, as place of origin before the Tertiary Era (S.W. China and N.E. Asia (East Angara) respectively). PAX (1885) previously supposed a circumpolar origin during the Tertiary Era. According to POJARKOVA, whose paper on the history of *Acer* is still the most important contribution, first migration of maples took place during the Eocene period by two paths: one along the north side of the Thetis and further northwards to Scandinavia, Greenland and N. America, the other southwards to the mountains of Central China and the Kunlun Mts. Simultaneously, there was also migration in the eastern direction and these taxa could meet those having migrated by the western paths, because during almost the whole of the Tertiary Era the access from eastern Asia to N. America and from there through the Atlantic into Europe was favorable.

According to PAX (1926) the maples already appeared in N. America during the Jurassic period. CHANEY (1949: quotation DESCHÊNES) and CROIZAT supposed this migration took place during the Cretaceous period, the latter assumed that they came across the Pacific Ocean in the same way as *Magnolia*. POJARKOVA supposed that the ancient *Tegmentosa* and *Ukurunduensia* (*Spicata* sensu POJARKOVA) penetrated from Europe, while *Rubra* and *Monspessulana* (*Goniocarpa*) reached Europe through N. America. In the history of the genus POJARKOVA distinguished three phases of development. After the first migration wave during the Eocene period the second phase followed in the middle of the Tertiary Era, during which a great number of new types was formed in the mountains of E. Asia. In view of the altered climatical conditions these taxa did not extend outside this region. In the same period in the eastern part of the Mediterranean region migration waves from northern Europe and central Asia met each other.

The third period in the history of *Acer* started at the beginning of the glacial periods (Pleistocene), which led to the extinction of most taxa in northern and central Europe (e.g. *Rubra*, *Palmata* and *Ukurunduensia*) and northern Asia. South eastern Asia, central China and Japan, where no drastic climatic changes occurred, retained many ancient species, N. America was well adapted owing to its geographic structure for the preservation of the ancient taxa. The present rather scanty representation of maples in eastern N. America shows that there never was a highly diverse maple flora in that area.

After the glacial periods, which broke the continuous areas of the ancient taxa, the final formation and fixation of the numerous geographic races occurred. The present species are said to originate from the Pliocene (POJARKOVA; STEBBINS, 1947; quotation DESCHÊNES).

PAX (1885) was the first to arrange phylogenetically the present taxa of the genus. His scheme was only based on the location of the disc (extrastaminal or intrastaminal) and the insertion of the stamens (hypogynous or perigynous). Reduction of the corolla and the diversity of the leaves were to him of secondary importance and regarded as the product of parallel evolutionary trends (see 7.3.2.1 and 7.3.4). KOIDZUMI (1911) somewhat altered PAX's scheme by distinguishing two main groups: the *Intra-staminalia* and the *Extra-staminalea*. POJARKOVA based her scheme on the close relationships of *Acer* to the *Sapindaceae* and further on the supposition that several ancient types were lost during the glacial period. In the conviction that within the *Sapindaceae* amphistaminal discs and lactiferous petioles are primitive, she considered *Platanoidea* and *Lithocarpa* as the most primitive sections. During the evolution of the genus the insertion of the stamens shifted to the inner margin of the disc. This development, already visible in series *Macrophylla*, led to the progenitors of sections *Acer* and *Trifoliata*. The remaining section differentiated from progenitors of *Acer* and have ancestors with more distant alliances. These relations are mostly uncertain after the extinction of their common ancestors. OGATA (1967) remarked that the absence of several ancient forms which may have linked the present sections made it difficult to know the correct interrelation of sections. He distinguished 6 groups which differ largely from one other phylogenetically:

Group A: Sections *Palmata, Macrantha, Parviflora, Glabra, Negundo, Ginnala* and *Rubra.*

Characters: small number of bud scales; leaves usually minutely serrate; woods soft and light and with more or less irregular fusiform rays. The heterogeneous section *Macrantha* was conjectured to be the nearest to the ancestor of this group. Section *Palmata* was rather remotely related to the remaining sections (extrastaminal disc; harder and heavier wood; less affinity of seed proteins (MOMOTANI 1962)). The compound leaves as found in section *Negundo* were thought to be derived from simple ones.

Group B: Section *Platanoidea.*

Group C: Section *Acer* (see 6.6.1 and 6.6.2).

Group D: Sections *Integrifolia, Trifoliata* and *Syriaca* (= series *Monspessulana* p.p.).

Taxa remotely related; high number of bud scales; disc extrastaminal.

Group E: Sections *Hyptiocarpa* and *Lithocarpa.*

Fairly closely related; inflorescences lateral and from leafless buds (except series *Macrophylla*); many imbricated bud scales; nutlets strongly convex.

Group F: Section *Indivisa.*

Leaves simple; wood rays very big.

7.3. PHYLOGENETIC DEVELOPMENTS OF MORPHOLOGIC CHARACTERS

7.3.1. *The inflorescences*

ALMSTEDT (1933: quotation HALL, 1951) presented a phylogenetic series of inflorescence types: (1) loose panicle (*A. pseudoplatanus*); (2) spike-like (*A. spicatum*): derived from the foregoing panicle by reduction of the rachis and flowers of lateral branches; (3) simple raceme (*A. pensylvanicum*): further reductions of secondary axis; (4) umbellate (*A. rubrum* and *A. saccharinum*): reduction of the rachis of the simple raceme. The inflorescences of *A. pseudoplatanus* can hardly be said to be loose panicles. ALMSTEDT probably referred to a different species (of series *Acer*?) to exemplify this type. TROLL (1964) interpreted the cincinni of *A. circinatum* and *A. palmatum* as derived from thyrsoid panicles such as occur in *A. platanoides.* The pronounced basitonous structure changed further by reduction of secondary branching and promoted development of cincinni in the lowest lateral branches. TROLL's interpretation seems to be based on an insufficient knowledge of the genus.

The inflorescences in *Acer* largely differ among themselves in structure and arrangement on the shoots. In chapter 2 five basic types and four modes of arrangement were distinguished.

The most original inflorescence is represented by type I (see fig. 1 and 16), which also occurs in primitive related taxa such as *Dipteronia, Aesculus* (*Hippocastanaceae*) and *Aporrhiza, Koelreuteria,* a.o. (*Sapindaceae*). This inflorescence represents a branched generative shoot with several cincinni. Reduction of the leaves led to the present appearance of this shoot as one compound inflorescence. This original inflorescence was erect and many-flowered. It developed terminally, and on vigorous shoots also laterally from mixed buds. The pedicels showed articulations which functioned as abscission places of blown ♂ flowers.

The large inflorescences were reduced in the genus to several other types (see fig. 1). A strong reduction of the rachis and secondary branching led to the small inflorescences as found in *A. circinatum* (type Ia). Most common was a reduction of the cincinni (type II). A further shortening of the secondary axes led to simple racemes (type III), which could further develop into umbels (type IV) by reduction of the rachis. The inflorescences of ♂ *A. negundo* specimens are for the second time in the evolution of the genus a product of a fusion, this time a compound raceme (see 2.3.2).

Besides this reduction of the inflorescences the portion of lateral inflorescences increased in several taxa (Group B) and finally all inflorescences could be laterally arranged (groups C and D) (see 2.3.2). With the exception of ♀ specimens in some taxa the latter development was also associated with a reduction of the leaves to budscales or bracts (group D).

7.3.2. *The flowers*

7.3.2.1. The perianth

Several authors, among them PAX (1885), HALL (1951) and OGATA (1967) regarded the 5-merous flower as original. Such flowers also predominantly occur in related taxa like *Dipteronia*, *Aesculus*, *Sapindaceae*. In a few taxa the flowers have a 6-merous perianth simultaneously showing an increase in the number of stamens to 9–13. In some other taxa the perianth became 4-merous, while the number of stamens decreased to 4–6 (see table 2).

The calyx and corolla of the original maple flowers were rather different in shape, pose, colour, hairiness and time of abscission. (see 2.2.3). This distinction, indicated by THORNE (1963) as original in *Angiosperms*, was considered as derived in *Acer* by MOMOTANI (1962).

The small, lobed, white petals as present in series *Sinensia* (see fig. 16) show features of a possible staminal origin, which LEINFELNER (1954, 1958) also supposed for the corolla of the *Sapindaceae*. The petals often changed strongly during the evolution of the genus. In some entomophilous taxa they became longer than the sepals, but more often they approached the sepals in appearance, especially in colour. In a number of taxa they became connate with the sepals, while in some anemophilous taxa the corolla was completely reduced or nearly so.

7.3.2.2. The androecium

It may be assumed that the original maple flower had already lost two stamens of the epipetalous whorl (see 2.2.4) because of the same incompleteness in primitive related taxa (*Dipteronia*, *Sapindaceae*). In some taxa, especially those with a 6-merous perianth, the number of stamens increased to 9-13, while in others, above all those with a 4-merous perianth, the epipetalous whorl is often completely reduced (see table 2). The observation, that stamens or anthers of blown ♂ flowers drop first (series *Sinensia*, *Ukurunduensia*, *Wardiana*) may show an original behaviour.

7.3.2.3. The honey disc

PAX (1885), KOIDZUMI (1911), NAKAI (1915), POJARKOVA (1933) considered the mode of staminal insertion on the disc as phylogenetically important. POJARKOVA assumed that an amphistaminal disc in *Sapindaceae* was the most common type, and ascribed this also to the *Aceraceae*. The common type in *Acer*, however, and further in *Aesculus*, *Dipteronia* and nearly all sapindaceous genera is extrastaminal and this type was certainly present in the original maple flowers.

The shift of stamen insertion to the middle or to the outer margin of the disc very probably started in more than one taxon, because the present taxa with amphi- or intrastaminal discs are partly remotely related (see table 2).

In some dioecious taxa, e.g. section *Indivisa* and series *Arguta* and *Cissifolia* the insertion of the stamens may vary between the outer margin and the middle of the disc, probably because some of the stamens became higher inserted, as a consequence of the absence of the (early aborted) pistil.

In two anemophilous taxa the honey disc is lost.

7.3.2.4. The pistil

All taxa of the *Aceraceae* predominantly have a bicarpellate ovary, while related taxa such as *Hippocastanaceae* and *Sapindaceae* usually have a tricarpellate ovary. This uniform condition in *Acer* does not need further discussion of its possible origin (see 2.2.1).

The evolution to amenophily was accompanied by an enlargement of the stigmatic surface, which resulted from a splitting of the style (see 2.2.6).

7.3.3. *The fruits and seeds*

Several taxa of the *Sapindaceae* have winged fruits, e.g. *Atalaya* and *Diatenopteryx*. The fruits of the latter genus occurring in S. America even strongly resemble the samaras of *Acer*. Within the *Sapindaceae* winged fruits are considered as derived (CORNER, 1954). The schizocarpic fruit of *Dipteronia* is less evolved than that of *Acer* (CORNER, 1954) and does not develop parthenocarpically (see fig. 2.1).

The ability of the fruits to grow parthenocarpically is a derived condition and seems combined with increased dormancy of the seeds (see 2.5.2 and 2.6.3). Parthenocarpy is nearly absent in the case of a rapid development of the embryo after fertilisation. The fruits, grown in this way have rather thin and weakly lignified pericarps, their seeds germinate immediately or show a slight degree of dormancy. These fruits are mainly developed in some taxa of S.E. Asia (section *Hyptiocarpa*, series *Sinensia*) and also in section *Rubra*. The fruits of the latter already ripen in early summer and their seeds germinate immediately. In the case of a strong parthenocarpic tendency the fruits have at first empty locules, which are filled by the growing embryo later on. Mostly, the pericarps are strongly lignified and the seed often does not germinate before the second spring after fruit ripening (e.g. section *Trifoliata* and series *Arguta*).

The parthenocarpic tendency occurs in remotely related taxa of the genus and may be developed independently in several taxa. It is always found in dioecious taxa and is less developed in taxa which flower relatively late during early summer or occur in subtropical areas.

The shape of the nutlet was found to be a rather important character for classification (OGATA, 1967). The present author also used this character in some cases to combine some series into sections (*Acer, Glabra, Integrifolia, Lithocarpa, Negundo* and *Platanoidea*). The fruits of *Acer* (except series *Acer*), *Integrifolia, Lithocarpa, Palmata* and *Trifoliata*, and *Indivisa* and *Negundo* show large resemblances. Similar resemblances exist between the fruits of series *Acer, Distyla* and *Parviflora and Tegmentosa* and *Ukurunduensia*.

7.3.4. *The leaves*

The variability of the leaves in *Acer*, which several taxonomists considered as very useful for classification (see 6.2), was hardly used in their phylogenetic concepts. PAX (1885) and OGATA (1967) supposed that compound leaves were derived from simple leaves. HAAS (1933) and PARKIN (1953) also regarded the simple, unlobed leaf as less evolved. HAAS supposed a continuous series from *A. carpinifolium* to the strongly palmately lobed *A. japonicum* (erroneously named *A. micranthum* by him). The pinnate leaves of *A. negundo* developed from this palmately lobed leaf by intercalary growth of the rachis. PARKIN used *Acer* as an example for showing that from a simple, oval-shaped, pinnately veined leaf all other forms could be derived. By lobing of the lamina to the base compound leaves could arise, while by interpolation of a rachis this would ultimately lead to a pinnate compound one.

The opposite view was held by TROLL (1935) and CORNER (1954). The former disagreed with HAAS suggesting that the palmately lobed leaf, derived from a basipetal pinnate leaf, was further reduced to an unlobed one. The same reduction was said to have happened also with the first pairs of leaves of seedlings and even with the cotyledons. CORNER came to his view because of regarding *Acer* as part of the 'Sapindalean Problem'. In his opinion, the acropetal pinnate leaf which is also found in *Dipteronia*, was the less evolved. In several taxa of the *Sapindaceae* these pinnate leaves had a prolonged rachis, shaped like a mucro, instead of a terminal leaflet. But with progressive reduction of apical growth a terminal leaflet was mostly developed and the number of leaflets could decrease to a trifoliolate and ultimately to a simple leaf as in *Dodonaea*.

The present author agrees with the latter concepts, except the derivation of the pedatinerved leaves with 7–13 lobes, as present in series *Palmata*, which may be a further specialisation. A remarkable fact in this connection is the omission of such leaves by TROLL from his series of reduction, which starts with a 5-lobed leaf of *A. pseudoplatanus*. In the paper of HAAS, from which TROLL borrowed the figures, leaf-pictures of *A. circinatum* and *A. japonicum* with 9 and 11 lobes were also present.

Heterophylly frequently occurs in *Acer* (CRITCHFIELD, 1971). An exception is formed by the sections *Indivisia* and *Hyptiocarpa* (?) and the series *Penninervia*. Most of the taxa with predominantly unlobed or 5-lobed leaves develop 3-lobed leaves as seedlings and on vigorous shoots. These 3-lobed leaves often are deeply lobed and any further lobation is very weak. Similar leaves usually also occur in fossils of the Middle European tertiary flora (WALTER, 1972). It may be possible that a stronger basipetal development of the side lobes has led to shortening of the lobes and an increase in the number of basical veins, and, consequently, in the number of lobes.

In figure 4 the different leaf types of *Acer* are shown. The arrows indicated the supposed developments, the dotted arrows are used to suggest that these developments probably did not occur in *Acer* or only in a few taxa.

The original maples were deciduous. The few evergreen taxa represent specialisations.

POJARKOVA (1933) considered lactiferous petioles, which also occur in the *Sapindaceae* as original. The present author agrees, especially after the observation of lactiferous petioles in *Dipteronia*.

7.3.5. *Bud scales and shoot development*

OGATA (1967) regarded the number of bud scales as very important when studying phylogenetic relationships of sections. He remarked in this connection that equal numbers could indicate close affinities, but that sections which largely differ in number of bud scales generally were remotely related to one another. There may be no doubt that the number of bud scales increased with the evolution of the genus. The related genus *Dipteronia* and most genera of the *Sapindaceae* still lack bud scales. The division of bud scale numbers in *Acer* is shown in table 2 (see also 2.5).

The taxa with few bud scales mainly concern fast growing, short-lived shrubs. The green or green-red colour of the young shoots is preserved for two to several years. The wood is mostly soft (OGATA, 1965, 1967). When during the summer shoot growth continues, only a part of the taxa, and mainly those with few bud scales, show continuous development of normal leaves. In the remaining taxa elongation stops, at least temporarily, after the expansion of the embryonic shoot in the winter bud and prolonged extensions growth is, or tends to be, discontinuous through the formation of disguised lamnas shoots (SPAETH, 1912; SCHUEPP, 1929; CRITCHFIELD, 1971). Taxa with a high number of bud scales are mainly found in arid regions, but sometimes also in tropical rain forests (*A. laurinum*). The suberization of the bast already starts in the first year.

7.4. EVOLUTION OF FLOWERING AND SEX EXPRESSION

The major trends in the evolution of flowering and sex expression in *Acer*, from entomophily to anemophily and from monoecy to dioecy, are very clear and were correctly described by PAX (1885), HALL (1951) a.o.. All authors referred in this connection to *A. negundo*, the single species of the genus in which both developments are completed. Chapter 3, and, to some extent, 4 and 5 provide materials to consider these developments. It was possible to distinguish 4 groups with different compositions of monoecious and dioecious individuals. (see 3.5). The most original mode of sex expression in *Acer* is duodichogamous i.e. a ♂-♀-♂ sex expression (flowering type C). It occurs in rather primitive taxa and also in primitive related taxa of the *Hippocastanaceae* and *Sapindaceae* and in *Dipteronia* (see 3.4). A strong mutual competition for nutritive and hormonal supply between the flower buds of the developing inflorescences led to pistil abortion in the major part of the flower buds and caused a rhythmic course of anthesis (♂-♀-♂). The time of appearance of the ♀ phase during anthesis was strongly governed by environmental conditions.

As first step to dioecy may be considered the appearance of protogynous flowering trees in such duodichogamous flowering populations (flowering type B). The ♀ sex expression of these specimens was less dependent on environmental conditions and provided the benefits of a hetero-dichogamous system, such as is found to-day in about 50% of the present species. The increase of protogynous individuals in the populations may be favoured by the decreasing size of the inflorescence, which led to the reduction of ♂$_{II}$ flowers (protandry) or even to reduction of the ♂$_{II}$ and ♀ phase (male flowering): flowering types D and E respectively.

Another early development in protandrous specimens was a genetically determined inability to produce ♀ flowers, i.e. the appearance of ♂ individuals. However, in a dichogamous system they could only occur in very low percentages. In any case ♂ individuals appeared much earlier during the evolution of the genus than ♀ individuals. The small number of ♀ flowers per inflorescence was a limiting factor for the origin of ♀ specimens. They could first appear in the populations after a further reduction of the inflorescences. At present there are taxa which have nearly completed the evolution to ♂ specimens, while besides ♀ specimens a considerable part within the populations is still protogynous. In such a stage, of evolution ecological conditions can determine the ratios of the various types within the populations. Such instability may exist for instance in *A. glabrum*, *A. monspessulanum*, *A. opalus*, *A. rubrum*, *A. saccharinum* and *A. saccharum*.

Besides some taxa which became completely dioecious, other taxa reached a more or less dioecious system by the incapacity to produce ♂$_{II}$ flowers combined with a strong reduction of the inflorescences to small racemes. All specimens are still basically protandrous, but environmental factors and the constitution of the specimens led to a predominantly dioecious sex expression as was concluded after studying some hundreds of herbarium specimens, collected at natural stands, and data in the literature. The absence of ♂$_{II}$ flowers and consequently of protogyny probably inhibited a similar course of evolution as elsewhere in the genus.

With the primitive monoecious condition the original maples already had a high pollen/ovule ratio, while further the size of the grains also provided a basis for an evolution to anemophily. A limiting factor was the stickiness of the grains which causes clumping of pollen into parcels too heavy for air transport. According to HAAS (1933) the pollen grains of anemophilous species *A. negundo* and *A. saccharinum* are still less dry than those of, for example, *Corylus*. *A. negundo* is the only completely anemophilous species. *A. saccharinum*, which lacks a honey disc, may be visited by pollen-collecting humble and honey bees in mild weather during anthesis. Another factor which promoted a development into anemophily was the migration to northern areas with shorter summer periods. This led to anthesis before the leaves were unfolded, which facilitates long distance dispersal of pollen.

Some other features of the present maples clearly indicate that anemophily contributes to pollination in various taxa. Several early flowering taxa have drooping inflorescences or drooping pedicels and flowers with an enlarged stigmatic surface.

The migration to temperate areas and the assimilation in other areas to conditions which shortened the vegetative period may have strongly influenced flowering and sex expression. Besides accelerated flowering it led to reductions in the size of the inflorescences and an increasing portion of axillary inflorescences, because the accelerated flower induction occurred before the terminal buds reached the generative stage. The shortening of the vegetative period also led to a very long time between flower induction and anthesis and a shift of sex differentiation to before bud burst. It may be possible that this accelerated sex differentiation promoted evolutional trends such as male flowering and protogyny and even complete dioecy.

STEBBINS (1951) stated that anemophily may often be responsible for the evolution of monoecy and dioecy in the *Angiosperms*. In *Acer* monoecy and dioecy are more original than anemophily, and probably provided a good basis for a development to anemophily in certain regions.

7.5. CONTRIBUTION OF THE REMAINING BIOSYSTEMATIC AND MORPHOLOGIC STUDIES

The studies of the seed proteins by MOMOTANI (1961) indicated affinities between series *Arguta* and *Glabra*, *Distyla* and *Parviflora*, *Acer* and *Monspessulana*, and further between sections *Glabra*, *Macrantha* (series *Tegmentosa*) and *Parviflora*. Rather remote from the other sections were *Indivisa*, *Negundo* and *Rubra*. TOWERS and GIBBS (1953) get similar reactions of series *Negundo* and *Cissifolia* and the genus *Dipteronia* in two different tests.

Karyological studies (see 6.6.3) showed that polyploidy is present in 3 groups of taxa without further affinities (sections *Indivisa* and *Rubra* and series *Acer*).

Species crosses and heteroplastic graftings sometimes succeeded with rather remotely related species, bud the incompleteness of these records limits their use in this connection.

Several other biosystematic studies, reviewed in 6.6, could have supplied very useful information, if more species, at least representatives of all series and sections, were involved. This also applies to palynological studies (see 2.2.8).

7.6. DISCUSSION AND CONCLUSIONS

The genus *Acer* probably dates from the end of the Paleozoic Era (CROIZAT, 1952: quotation DESCHÊSNLES, 1971).

The ancestors were short-lived trees and shrubs of the tropical rain forest and probably very close to ancestors of the tribe *Harpullieae* of the *Sapindaceae* (LEENHOUTS, personal communication). The place of origin may be S.W. China as suggested by PAX (1926) or more southern (CROIZAT).

A northern migration route brought the maples to N.E. Asia and western N. America (series *Glabra* and *Macrophylla*). A further northern migration from Asia gave the genus a circumpolar distribution at the beginning of the Tertiary Period. It is likely that at that time the major developments of the genus were already finished and all modern sections were formed (POJARKOVA).

Not all these sections were capable of migrating from N.E. Asia to the arctic regions and from there or directly from N.E. Asia to N. America and Europe. This hypothesis may be illustrated by the present distribution of the genus in N. America (POJARKOVA). Assuming that 2 series (*Glabra* and *Macrophylla*) reached the western coast through the Pacific, only representatives of 6 other series have been conserved up till now. It is, however, generally accepted that the geographic constitution of N. America was very appropriate for the Tertiary flora to survive the glacial periods.

In Europe and W. Asia only 3 sections are represented today. The glacial periods could have caused the extinction of several taxa, but palaeologic studies of the Tertiary maple flora indicated that complete extinction of sections in Europe only concerns *Palmata* (few records) and *Rubra*, and series *Saccharodendron* (WALTER, 1972) and probably series *Ukurunduensia* (POJARKOVA). POJARKOVA supposed that series *Monspessulana* and *Saccharodendron* reached Europe by an eastern migration route. The close affinities of these series to series *Acer*, however, make a migration from Europe to N.E. America of series *Saccharodendron* more likely. Accepting a second phase of development in E. Asiatic maples during the middle of the Tertiary, which period was rather unfavorable for migration outside that area (POJARKOVA) may explain the limited distribution of several highly specialised taxa such as series *Arguta*, *Cissifolia* and *Lithocarpa*. According to PAX (1885) and POJARKOVA the final formation of the numerous subspecies and varieties already dates from the Pleistocene.

In the present taxa of the genus several phylogenetic trends can be observed. Most important in this connection are the inflorescences, flowers, bud scales and mode of sex expression and also leaves, fruits and seeds. As a result of these studies, summarized in the preceding paragraphs, the original maple can be described as a short-lived, deciduous tree or shrub with pinnate leaves, lactiferous petioles, and up to two pairs of bud scales; large terminal and lateral inflorescences with cincinni (type I) and articulated pedicels; 5-merous flowers with a distinct calyx and corolla, 8 stamens and an extrastaminal disc; fruits with a low parthenocarpic tendency, an unlignified pericarp and a globular nutlet; seeds without dormancy, with an epigeal germination and narrowly oblong cotyledons. The trees flowered duodichogamously (♂-♀-♂; flowering type C) and anthesis started several weeks after bud burst. Present taxa, which are closest to this original maple, are representatives of sections *Palmata* and *Parviflora* and more particularly: *A. spicatum*, *A. tonkinense* and *A. nipponicum.*

Several authors presented phylogenetic schemes of the genus, mostly based on a small number of morphological characters. The present author has long cherished the hope that the results of his detailed morphologic and biosystematic studies would support sufficient data for a more definitive phylogenetic scheme as a crown on his studies. But these data are still insufficient, not only by the missing links of extinct taxa but more especially by the frequent occurrence of similar developments in different taxa (parallel evolution). A better view of the phylogenetic relationships of the present taxa may be obtained by further palynological and biosystematic studies, notably chemistry.

The lack of a phylogenetic scheme does not mean that it would not be appropriate to make some personal remarks on the phylogenetic relationships of the present sections:

I. Section Acer

The series *Monspessulana* and *Saccharodendron* are more specialised than the series *Acer* (leaves, reduction of the corolla, sex expression, anemophily, parthenocarpy).

The section appears rather related to *Integrifolia* and *Trifoliata* and rather remotely related to *Ginnala, Lithocarpa* and *Platanoidea.* Relationships with all taxa with 5 and more bud scales may exist, except with *Indivisa.*

II. Section Platanoidea

The affinities of both series, which are only based on morphologic similarities, need further study. The lactiferous petioles and the amphistaminal disc of series *Platanoidea* and *Macrophylla* probably only indicate a remote relationship. The rather primitive section does not show close affinities to other sections (see under I. section *Acer*).

III. Section Palmata

The whole section and especially series *Sinensia* is primitive. The latter series only deviates from the original maple described above by the aborted terminal buds, the lobed leaves and the 4 pairs of bud scales. On the basis of morphological characters this section is very close to section *Parviflora*, but this could not be established by the experiments of MOMOTANI (1962), who, however, only studied some species of the more specialised series *Palmata*. Probably the section had already been somewhat distinct from the remaining taxa from the early times of the genus.

IV. Section Macrantha

The relation of both series is only based on morphologic characters of leaves, bud scales and fruits. Series *Tegmentosa* is rather close to the primitive series *Parviflora*, which may be near the ancestors of the former series.

V. Section Parviflora

All series and especially *Ukurunduensia* show the characters of the original maple except the leaves. Relationships to sections *Glabra* and *Macrantha*.

VI. Section Trifoliata

Rather specialised taxon with primitive leaves (trifoliate). The 6-merous perianth possibly indicates a closer relationship with *Lithocarpa*. Further affinities to *Acer* and *Integrifolia* (see also under I. *Acer*).

VII. Section Rubra

Highly specialized section with unclear relationships. Morphologically some similarities with section *Glabra*, series *Pubescentia* and even section *Hyptiocarpa* (lateral inflorescences, reduction of stamens, disc, seedlings (*Pub.*) and fruit *Hypt.*)).

VIII. Section Ginnala

Rather primitive section without clear relationships. Somewhat related are probably *Acer* and *Integrifolia*.

IX. Section Lithocarpa

The section comprises the rather primitive series *Macrophylla* and the specialized series *Lithocarpa*. Relationships with *Acer*, *Trifoliata*, *Integrifolia* and possibly with *Hyptiocarpa* and *Platanoidea*.

X. Section Negundo

Two highly specialized, closely related series, which still have the original pinnate leaves and a low number of bud scales. The affinities to other sections are not very clear. The section probably represents a very early specialized taxon.

XI. Section Glabra

This section resembles *Lithocarpa* in specialisation and geographic distribution. Both have a rather primitive monotypic series in western N. America and a more specialized, dioecious series in E. Asia. Affinities to *Parviflora* and perhaps to *Macrantha*.

XII. Section Integrifolia

The two series mainly vary in their leaves, but the monotypic series *Pentaphylla* is very little known. Affinities to *Acer*, *Ginnala*, *Trifoliata* and *Lithocarpa* (see under I. *Acer*).

XIII. **Section Indivisa**

The most specialized section of the genus (dioecious, unlobed leaves, simple racemes, many bud scales, tetraploid) without clear affinities to any other section. The fruits resemble those of section *Negundo*, but parthenocarpic fruits are flat.

XIV. **Section Hyptiocarpa**

Highly specialized section. Affinities indistinct (*Lithocarpa* and *Trifoliata*?).

SUMMARY

The genus *Acer*, the maple, shows a large diversity in morphological characters, flowering and sex expression. The genus includes more than 110 species, which mainly occur in temperate regions of the northern hemisphere. In the southern Himalayas maples occur up to elevations of 3300 m., while one taxon reaches the mountains of some of the largest islands of the Indonesian and Philippine Archipelago.

The morphology was found to be insufficiently described. Detailed studies were made of the reproductive organs (chapter 2). The evolutional trends of several morphological characters were discussed in Chapter 7. Of the 5 basic types of inflorescences the compound inflorescence, of which the secondary or tertiary axes branch further into cincinni, was found to be original in *Acer* and related genera. The pedicels of the flowers in such cincinni sometimes showed articulations at the place of future abscission. The most common inflorescence in *Acer* was derived from this type by reduction of the cincinni. Further reduction led to racemes and umbels.

The arrangement of the inflorescences on the shoots developed from mixed terminal to leafless lateral buds. In the case of vigorous shoots of ♂ individuals of *A. negundo* ramification within the leafless lateral bud led to the occurrence of compound racemes.

Original characters of maple flowers are the 5-merous perianth with a distinct calyx and corolla, the extrastaminal honey disc and 8 stamens. As derived may be considered 4- or 6-merous flowers with 4–6 and 8–12 stamens respectively, an amphistaminal disc and, as a further specialisation, an intrastaminal disc. Other developments were the occurrence of parthenocarpy and an increase in the number of bud scales from 2 pairs to 11–15 pairs.

The leaves are very characteristic and 9 leaf types are distinguishable. The less frequent pinnate leaf is indicated as the more original leaf. Most common are trilobate and palmately lobed leaves, while unlobed leaves are regarded as a further specialisation.

For an analysis of flowering and sex expression more than 1000 trees were observed during 3–5, and sometimes up to 10 years and several hundred herbarium specimens of uncultivated taxa were studied in some of the largest herbaria (chapter 3). For a good interpretation of the sex expression more detailed information on sex differentiation was needed. For this purpose a study was made on flower morphogenesis (chapter 4) and a number of physiological experiments were carried out (chapter 5). On the basis of their sex expression the taxa could be divided into 5 groups, representing the original mode of sex expression, three stages of development to dioecy and complete dioecy:

1. Dichogamous taxa which mainly flower with a ♂-♀-♂ sequence of phases (duodichogamy). The aborted pistils of ♂ flowers which have their anthesis

before the ♀ phase (♂$_{\mathrm{I}}$ flowers), are smaller than those of ♂ flowers after the ♀ phase (♂$_{\mathrm{II}}$ flowers). The sex differentiation of the ♂$_{\mathrm{I}}$ flowers probably occurs between bud burst and about one week before the beginning of anthesis of the inflorescence and may be caused by competition of the developing younger parts of the inflorescence and further by environmental factors. The differentiation of ♂$_{\mathrm{II}}$ flowers is regulated by competition of ♀ buds and ♀ flowers and takes place within the last two weeks before their anthesis. This competition was shown by removal of ♀ buds during a number of days after bud burst (*A. pseudoplatanus*). The ♀ flowers show functional male sterility: the anthers fail to release pollen. This failure may be caused by an inhibitor produced by the pistil. Both the time of appearance and the number of ♀ flowers are influenced by environmental conditions. A late appearance led to protandry (♂-♀); a complete lack to ♂ flowering (≠ ♂ individuals). Protogynous (♀-♂) flowering individuals form less than 10% of the populations.

This mode of sex expression, which is also present in primitive related taxa such as *Dipteronia* (*Aceraceae*), *Aesculus* (*Hippocastanaceae*) and several sapindaceous genera, is considered as the original mode of sex expression in *Acer*. Representatives of this group are the series *Parviflora*, *Sinensia* (partly) and *Ukurunduensia*. Further characteristics of these taxa are the large compound inflorescences with cincinni, mainly developed from mixed terminal buds; the small entomophilous flowers with distinct calyx and corolla; the beginning of anthesis one month after bud burst or later; the low parthenocarpic tendency; the low number of bud scales.

2. Dichogamous taxa of which about half the population flowers protogynously and the remaining individuals produce, protandrous, duodichogamous and/or male inflorescences (heterodichogamy). Protogyny in most taxa is to a large extent genetically controlled. Few ♂$_{\mathrm{I}}$ flowers were occasionally observed in the lower parts of the crown. The appearance of these protogynous individuals in the populations may be seen as a first step to the development of ♀ individuals. These individuals changed the environmentally controlled duodichogamous system into a heterodichogamous system, which favoured cross pollination more strongly. The remaining part of the populations differ from those of group 1 by the smaller inflorescences, which led to a reduction in the number of phases, so the proportion of protandry and ♂ flowering is higher. The appearance of the ♀ phase is still largely controlled by environmental factors. This gave rise to annual variations and also to variations within the individual trees, especially when inflorescences are also produced in vigorous shoots of the previous year. The latter inflorescences sometimes flower protogynously.

Anthesis starts simultaneously with or shortly after bud burst. The sex differentiation of ♂$_{\mathrm{I}}$ flowers occurs between 1–5 months before anthesis. The cause of the pistil abortion is unclear. Probably the oldest buds have insufficiently competitive power. This differentiation could not be established accurately by observations on pistil development because the aborted pistil showed some further development. It was found that when detached branches were forced into flower during the winter months sex differentiation of ♂$_{\mathrm{I}}$ flowers stopped immediately. Consequently accelerated flowering could be used as an aid studying the progress of sex differentiation in the tree outdoors. It was further found that auxins and gibberellic acid did not influence the ultimate sex expression in the experiments, but only broke the dormancy of the branches.

Genetic ♂ individuals, if present, form a very low percentage of the population. They probably have few possibilities to increase during this heterodichogamous stage.

This mode of sex expression is most common in the present taxa and occurs in the sections *Platanoidea*, *Palmata* (partly), *Ginnala*, *Integrifolia* and the series *Acer*, *Distyla*, *Macrophylla* and *Saccharodendron*.

3. A group which is intermediate between the preceding and the completely dioecious group. The protogynous individuals are partly replaced by ♀ individuals. The ratios vary between the species and the populations of a species. The evolution to ♂ individuals is completed or nearly so. In the latter case protandry still occurs, but the small inflorescences tend to flower completely male in most years. Protogynous individuals often also produce few if any ♀ flowers. Although the data are rather incomplete for this group, it is clear that the evolution to ♂ individuals is finished much earlier than that to ♀ individuals. The sex differentiation of ♂$_{\mathrm{I}}$ flowers (of ♂ specimens) occur within some months of initiation and more than 5 months before anthesis. This was concluded both from observations on pistil development and from forcing experiments.

Taxa of this group are the sections *Rubra* and *Hyptiocarpa* and the series *Glabra* and *Monspessulana*. All these taxa tend to develop lateral inflorescences, often flower before leaf development and show various stages of development to anemophily.

4. A basically protandrous flowering group, of which the individuals are unable to produce ♂$_{\mathrm{II}}$ flowers and in which protogyny was never observed. The inflorescences are small racemes, which usually produce unisexual flowers of one type only. According to data in the literature and the herbarium specimens studied the individual trees mainly flower completely ♂ or ♀ in their natural habitats. Observations on cultivated trees during periods of up to ten years showed that all trees were able to produce flowers of both sexes. Androgynous inflorescences, if present, always flowered protandrously. The sex expression appeared to be strongly dependent on environmental and internal factors. The ♂ and ♀ flowers on one tree were often distributed over separate branches. These branches could flower simultaneously and self-pollination (geitonogamy) occurred. Detached branches of some ♂ flowering trees flowered completely ♀ if forced into flower till one month before anthesis outdoors.

This mode of sex expression is present in series *Tegmentosa* and *A. maximowiczianum* (syn. *A. nikoense*) and probably was an early specialisation. It was observed that in series *Parviflora* (group 1), which is closely related to series *Tegmentosa*, ♂$_{\mathrm{II}}$ flowers are not very numerous.

5. Dioecious taxa, represented by the sections *Indivisa* and *Negundo* and the series *Arguta* and *Lithocarpa*, altogether less than 10 per cent of the species

of the genus. With the exception of section *Indivisa*, in which the ♀ flowers have rudimentary stamens, ♀ flowers lack stamens. Male flowers mostly show small abortive pistils. The inflorescences are strongly reduced and, with the exception of section *Indivisa* and ♀ specimens of series *Arguta*, are exclusively produced in (nearly) leafless lateral buds. Unpollinated ♀ flowers of all taxa develop parthenocarpically.

Besides the evolution to dioecy the maples show trends to anemophily. This development seems to have been favoured by the climatical conditions in certain parts of the area and is most pronounced in the early flowering taxa of eastern N. America, where one taxon, series *Negundo*, is completely anemophilous.

The results of the above studies were useful aids in revising the infrageneric classification (chapter 6). The present author distinguished in *Acer* 14 sections, of which 9 were subdivided into 2 or 3 series. Of these, the monotypic series *Wardiana* is a new one, while the name *Ukurunduensia* replaces an invalid name. A diagnosis of and a key to all sections and series are given. The phylogenetic relationships of these were briefly discussed. These relationships are not yet fully clear. A handicap is mainly formed by the many parallel developments within the genus.

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SAMENVATTING

Het geslacht *Acer*, de esdoorn, is zeer variabel in zijn morfologische kenmerken, bloei en geslachtsexpressie. Het telt meer dan 110 soorten, die voornamelijk voorkomen in de gematigde streken van het noordelijk halfrond. In het zuidelijke gedeelte van de Himalaya komen ze voor tot op een hoogte van 3300 m. Eén taxon heeft een verspreidingsgebied dat vanaf de Z.O. Himalaya reikt tot de gebergten van een aantal van de grootste eilanden van de Indonesische en Philippijnse archipel.

Een onderdeel van deze studie vormde de morfologie, met name die van de generatieve organen en was vooral noodzakelijk door het onvolledige beeld dat de literatuur verschafte (Hoofdstuk 2). De ontwikkelingslijnen van verschillende morfologische kenmerken werden besproken in Hoofdstuk 7. Van de 5 basis typen kon als de oorspronkelijke bloeiwijze van *Acer* en verwante geslachten worden aangewezen een samengestelde bloeiwijze, waarvan de secondaire en tertiaire zijassen zich verder vertakken tot schichtjes. De bloemsteeltjes van dergelijke schichtjes vertoonden soms insnoeringen op de plaats van het uiteindelijke breukvlak. Het type bloeiwijze dat thans het meest verbreid is in het geslacht ontstond uit het bovengenoemde, na verkorting van de schichtjes. Een verdere afname van de vertakkingen leidde tot trossen en schermen. De rangschikking van de bloeiwijzen aan de takken ontwikkelde zich van overwegend eindstandig tot uitsluitend okselstandig. In laatst genoemd ontwikkelingsstadium verschijnt de bloeiwijze meestal uit een bladloze knop. In okselknoppen aan langloten van ♂ individuen van *A. negundo* kan een verdere vertakking plaats vinden in de oksels van de knopschubben, die leidt tot een samengestelde tros.

Als oorspronkelijke kenmerken van de bloem kunnen beschouwd worden de vijftallige perianth met duidelijk onderscheiden kelk en kroon, de extrastaminale discus (honingschijf) en het bezit van 8 meeldraden. Vier- of zestallige bloemen met respectievelijk 4–6 en 8–12 meeldraden zijn secondaire ontwikkelingen, evenals het optreden van een amphistaminale discus, die op zijn beurt weer kon ontwikkelen tot een intrastaminale discus. Andere ontwikkelingen waren het optreden van parthenocarpie en een toename van het aantal knopschubben van 2 paar tot 11–15 paar. Het blad is zeer gevarieerd van vorm en een negental typen kon worden onderscheiden. Hiervan werd het weinig voorkomende geveerde blad aangeduid als het meest oorspronkelijke esdoornblad. Het thans meest algemene bladtype is handnervig met meestal 3 of 5 lobben. De ongelobde veernervige bladeren worden beschouwd als een verdere specialisatie.

Teneinde te komen tot een analyse van de bloei en de geslachtsexpressie werden waarnemingen verricht aan meer dan 1000 bomen gedurende 3–5 jaar, soms zelfs 10 jaar lang. Vele honderden herbarium specimens, vooral van niet in cultuur zijnde taxa, werden bestudeerd in enkele van de grootste herbaria (Hoofdstuk 3). Voor een goede interpretatie van de geslachtsexpressie was meer kennis nodig van de geslachtsdifferentiatie. Hiervoor werd een studie gemaakt van de aanleg en de ontwikkeling van bloemknoppen (Hoofdstuk 4) en werden een aantal fysiologische proeven gedaan (Hoofdstuk 5). Op grond van hun geslachtsexpressie werden de taxa ingedeeld in 5 groepen. De eerste hiervan vertoont (of benadert) nog de oorspronkelijke bloei, de volgende 3 kunnen gezien worden als ontwikkelingsstadia naar tweehuizigheid, terwijl de 5e groep volledig tweehuizig is:

1. De taxa vertonen overwegend een ♂-♀-♂ volgorde van de geslachten tijdens de bloei. Deze vorm van dichogamie kan aangeduid worden als duodichogamie. De geaborteerde stampers van de ♂ bloemen, die bloeien voor de ♀ fase (♂$_{\mathrm{I}}$ bloemen) zijn kleiner dan die van ♂ bloemen na de ♀ fase (♂$_{\mathrm{II}}$ bloemen). De geslachtsdifferentiatie van ♂$_{\mathrm{I}}$ bloemen vindt waarschijnlijk plaats tussen het opengaan van de gemengde knoppen en ongeveer een week vòòr de bloeiwijze in bloei komt. De vermoedelijke oorzaken van de stamperabortie zijn, de concurrentie van de zich ontwikkelende jongere delen van de bloeiwijze alsmede milieufactoren. De geslachtsdifferentiatie van ♂$_{\mathrm{II}}$ bloemen wordt bepaald door concurrentie van ♀ knoppen en ♀ bloemen en vindt plaats in de laatste 14 dagen voordat ze in bloei komen. Deze concurrentie kan worden aangetoond door de ♀ knoppen van bloeiwijzen te verwijderen gedurende een aantal dagen na het ontluiken (*A. pseudoplatanus*). De ♀ bloemen vertonen functionele mannelijke steriliteit: de helmhokjes blijven gesloten, waardoor geen pollen vrij komt. Als oorzaak hiervan wordt een door de stamper geproduceerde remstof verondersteld. Zowel het tijdstip van verschijnen van de ♀ bloemen tijdens de bloeiperiode als het aantal ♀ bloemen wordt beïnvloed door milieufactoren. Indien deze ♀ bloemen erg laat verschijnen is er sprake van protandrie (♂-♀) en indien zij ontbreken van ♂ bloei (niet van een ♂ individu). Protogynisch (♀-♂) bloeiende individuen vormen minder dan 10% van de populaties.

Deze oorspronkelijke wijze van geslachtsexpressie, die ook voorkomt bij primitieve verwante geslachten zoals *Dipteronia* (*Aceraceae*), *Aesculus* (*Hippocastanaceae*) en verschillende geslachten van de *Sapindaceae*, wordt in *Acer* aangetroffen in de series *Parviflora*, *Sinensia* (gedeeltelijk) en *Ukurunduensia*. Deze taxa worden verder gekenmerkt door grote samengestelde bloeiwijzen met schichtjes uit gemengde, overwegend eindstandige knoppen; kleine door insecten bestoven bloemen met een duidelijk onderscheiden kelk en kroon; een bloeiperiode, die een maand na het ontluiken begint of later; een geringe neiging tot parthenocarpie en een gering aantal knopschubben.

2. De taxa hebben een vorm van dichogamie, die kan worden aangeduid als heterodichogamie. Ongeveer de helft van de populatie bloeit protogynisch, de overige individuen hebben protandrische, duodichogame en/of ♂ bloeiwijzen. Protogynie is in de meeste taxa vrij sterk genetisch gefixeerd. Slechts bij uitzondering werden nog enkele ♂$_{\mathrm{I}}$ bloemen waargenomen, steeds aan laaggeplaatste takken. Het verschijnen van deze protogynische individuen in de populaties kan gezien worden als een eerste stap naar de ontwikkeling van ♀ individuen. Eerstgenoemden veranderden het door milieufactoren gecontroleerde duodichogame systeem in een heterodichogaam systeem, wat veel gunstiger was voor kruisbestuiving.

Het resterende, niet protogynisch bloeiende deel van de populaties verschilt van groep 1. door de kleinere bloeiwijze, en dientengevolge door een kleiner aantal geslachtsfasen. Hierdoor nam het aandeel van protandrie en geheel ♂ bloei sterk toe. Het verschijnen van de ♀ fase tijdens de bloeiperiode wordt nog grotendeels door milieufactoren bepaald. Het bloeiritme vertoont verschillen in de opeenvolgende jaren. Ook de bloeiwijzen van een individuele boom, vooral als er ook bloeiwijzen ontwikkeld worden aan langloten van het voorafgaande jaar, kunnen sterk verschillen in bloeiritme. Een gedeelte van laatstgenoemde bloeiwijzen kan zelfs protogynisch bloeien.

De bloei begint tijdens of kort na het ontluiken. De geslachtsdifferentiatie van ♂$_{\mathrm{I}}$ bloemen vindt plaats 1–5 maanden vòòr de bloei. De oorzaak van de stamperabortie is onduidelijk. Vermoedelijk hebben de oudste bloemknoppen een slechtere concurrentiepositie. Het tijdstip van stamper abortie kon niet goed worden waargenomen, omdat ook na de abortie de stamper nog enige groei blijft vertonen. Dit tijdstip kon echter wel vastgesteld worden door afgesneden takken in bloei te forceren. Tijdens dit forceren vond geen verdere uitbreiding van de ♂$_{\mathrm{I}}$ fase meer plaats, zodat het forceren van takken op verschillende tijdstippen de mogelijkheid bood de voortgang van de geslachtsdifferentiatie van ♂$_{\mathrm{I}}$ bloemen buiten in de boom te bestuderen. Bij deze experimenten bleken auxinen en gibberellinezuur, nodig voor de rustverbrekende werking, geen invloed te hebben op de geslachtexpressie.

Genetisch ♂ individuen maken, voor zover aanwezig, slechts een zeer klein percentage van de populatie uit. Ze hebben waarschijnlijk maar geringe mogelijkheden om in aantal toe te nemen in een heterodichogaam systeem.

Deze wijze van geslachtsexpressie is in de huidige taxa het sterkst verbreid en komt voor in de secties *Platanoidea*, *Palmata* (gedeeltelijk), *Ginnala*, *Integrifolia* en de series *Acer*, *Distyla*, *Macrophylla* en *Saccharodendron*.

3. Een groep die enigszins intermediair is tussen de voorafgaande en de volledige tweehuizige groep. De protogynisch bloeiende individuen zijn gedeeltelijk vervangen door ♀ individuen. De aantalsverhoudingen verschillen van soort tot soort en binnen eenzelfde soort van populatie tot populatie. De evolutie tot ♂ individuen is voltooid of bijna voltooid. In het laatstgenoemde geval kan er nog sprake zijn van protandrie, maar de kleine bloeiwijzen bloeien veelal volledig ♂. Ook protogynisch bloeiende individuen produceren vaak weinig of geen ♂$_{\mathrm{II}}$ bloemen.

De gegevens van deze groep zijn nog onvolledig. Duidelijk is wel dat de genetisch ♂ individuen eerder verschenen dan ♀ individuen en tijdens de verdere evolutie bleef hun aantal in de populatie ook steeds groter.

De geslachtsdifferentiatie van ♂$_{\mathrm{I}}$ bloemen (van ♂ individuen) vindt binnen enkele maanden na de bloemaanleg plaats. Dit is meer dan 5 maanden voor de uiteindelijke bloei. De stamperabortie kon worden waargenomen en ook forceerproeven toonden deze vroege differentiatie aan.

Taxa van deze groep zijn de secties *Rubra* en *Hyptiocarpa* en de series *Glabra* en *Monspessulana*. Deze taxa vertonen allen een tendens om overwegend of zelfs uitsluitend laterale bloeiwijzen te ontwikkelen. Ze bloeien vaak vòòr de bladontwikkeling en vertonen ook verder uiteenlopende ontwikkelingsstadia naar windbestuiving.

4. Een naar genetische aanleg protandrische groep, waarvan de individuen geen ♂$_{II}$ bloemen voortbrengen en waarin protogynie nooit werd waargenomen. De bloeiwijzen zijn kleine trossen, die gewoonlijk slechts één type eenslachtige bloemen produceren. Afgaande op de literatuurgegevens en de bestudeerde herbarium-specimens bloeien de afzonderlijke bomen op hun natuurlijke standplaatsen gewoonlijk volledig ♂ of ♀ .Waarnemingen aan gekweekte bomen, in enkele gevallen gedurende 10 jaar, wezen uit dat alle bomen in staat waren om bloemen van beiderlei sexe voort te brengen. Wanneer laatstgenoemde bloemen in dezelfde bloeiwijze voorkwamen, verliep de bloei steeds protandrisch. De geslachtsexpressie bleek sterk gereguleerd te worden door milieufactoren en door inwendige factoren van de boom zelf. De verdeling van de ♂ en ♀ bloemen binnen een boom was vaak taksgewijs. Deze takken konden gelijktijdig bloeien en zo aanleiding geven tot zelfbestuiving (geitonogamie). Afgesneden takken van enkele ♂ bloeiende bomen bloeiden volledig ♀ wanneer ze in bloei geforceerd werden tot één maand voor de bloei buiten.

Deze wijze van geslachtsexpressie komt voor in de serie *Tegmentosa* en in *A. maximowiczianum* (syn. *A. nikoense*) en betreft waarschijnlijk een vroege specialisatie. Enige aansluiting geeft de aan *Tegmentosa* verwante serie *Parviflora* (groep 1), waar het aantal ♂$_{II}$ bloemen slechts gering is.

5. Een groep tweehuizige taxa, gevormd door de secties *Indivisa* en *Negundo* en de series *Arguta* en *Lithocarpa*, tesamen met minder dan 10 percent van de soorten van het geslacht. Met uitzondering van sectie *Indivisa*, waarin de ♀ bloemen rudimentaire meeldraden bezitten, hebben de ♀ bloemen geen meeldraden. De ♂ bloemen vertonen meestal kleine rudimentaire stampers. De bloeiwijzen zijn sterk gereduceerd en worden met uitzondering van sectie *Indivisa* en ♀ individuen van serie *Arguta* uitsluitend ontwikkeld uit (±) bladloze okselknoppen. Onbestoven ♀ bloemen ontwikkelen zich parthenocarp.

Naast deze ontwikkelingen naar tweehuizigheid vertoont *Acer* ontwikkelingen naar windbestuiving. Deze ontwikkelingen lijken gestimuleerd te zijn door de klimatologische omstandigheden in bepaalde delen van het areaal en zijn het meest duidelijk in de vroeg bloeiende soorten van N.O. Amerika, waar één soort, *A. negundo* volledig anemofiel is.

De resultaten van bovengenoemde studies droegen veel bij tot een revisie van de classificaties binnen het geslacht (Hoofdstuk 6). In *Acer* werden 14 secties onderscheiden, waarvan er 9 verder werden onderverdeeld in 2 of 3 series. Van deze series werd de monotypische serie *Wardiana* beschreven als een nieuwe serie, terwijl de benaming *Ukurunduensia* een ongeldige naam moest vervangen. Bij deze nieuwe indeling werd een diagnose opgenomen van alle onderscheiden eenheden en een determinatiesleutel. De phylogenetische betrekkingen van de taxa werden kort besproken (Hoofdstuk 7). Deze betrekkingen zijn vooralsnog slechts ten dele duidelijk. Een belemmering vormen vooral de vele parallelle ontwikkelingen binnen het geslacht.

REFERENCES

ALMSTEDT, M. F. (1933). An anatomical study of the inflorescence of certain species of *Acer*. Cornell University (thesis)17 pp. (quotation HALL, 1951).

ANDERSON, N. J. F. (1964). A comparative study of the vegetative and the floral apex of *Acer pseudoplatanus* L. Diss. Abstr. **25**, 2: 772.

BANERJI, M. L. and S. DAS (1971). *Acer* in Nepal. Indian For. **97**, 5: 243–250.

BAWA, K. S. (1974). Breeding systems of tree species of a lowland tropical community. Evolution **28**: 85–92.

BEAN, W. J. (1970) Trees and shrubs hardy in the British Isles. *Acer*. 8th ed., **1**:185–240. London.

BELOSTOKOV, G. P. (1961). [Structure of the generative shoots of *Acer negundo* L.]. Bot. Žur. **46**, 6: 863–869.

BENSELER, R. W. (1969). Studies in the reproductive biology of *Aesculus californica* (Spach) Nutt. Univ. of California (thesis). Ann Arbor. 163 pp.

BENTHAM, G. and J. D. HOOKER (1862). Genera plantarum and exemplaria imprimis in herbariis kewensis servata definita I.: 409. London.

BESKARAVAJNAJA, M. A. (1971). [Morphological features of the flowers and the biology of flowering in different species of *Acer*] Trudy, Gos. Nikitsii Bot. Sad **44**: 161–169.

BLOEMBERGEN, S. (1948). *Aceraceae*. In: Addenda, corrigenda et emendenda. Fl. Mal. **I**, **4**: 3–4.

BOEHMER, G. R. (1760). In: C. LUDWIG: Definitiones Generum Plantarum, e.d. **3**: 508. Leipzig.

BOOM, B. K. (1965). Flora der cultuurgewassen van Nederland I. Nederlandse Dendrologie, ed. 5: 308–319. Wageningen.

BOUCHÉ, C. D. (1879). In: E. REGEL, Notizen, Gartenflora **28**: 61–63.

BRAUN, A. (1864). In: ASCHERSON, P. Flora der Provinz Brandenburg, der Altmark und des Herzogtums Magdeburg I: 52. Berlin.

BROWN, D. S. (1957). The rest period of apricot flower buds as described by a regression of time of bloom on temperature. Plant Physiol. **32**, 2: 75–85.

BROWN, D. S. and F. A. KOTOB (1957). Growth of flower buds of apricot, peach and pear during the rest period. Proc. Amer. Soc. Hort. Sci. **69**: 158–164.

BUCHENAU, F. (1861). Morphologische Bemerkungen über einige *Acerineen*. Bot. Zeit. **19**: 265–269, 273–278 and 281–286.

CARL, C. M. and H. W. YAWNEY (1972). Multiple seedlings in *Acer saccharum*. Bull. Torrey Bot. Club **99**: 142–144.

CHANEY, R. W. (1947). Tertiairy centers and migration routes. Ecol. Monog. **17**: 139–148. quotation DESCHÊNES, 1970).

CHATIN, A. (1874). Organogénie comparée de l'androcée dans ses rapports avec les affinités naturelles (classes des *Polygalinées* et des *Aesculinées*). C. R. hebdomadaires des séances de l'Academie de Paris **78**, 18: 1280–1284.

CORNER, E. J. H. (1954). The Durian theory extended – II. The arillate fruit and the compound leaf. Phytomorphology **4**: 152–165.

CORRENS, C. (1928). Bestimmung, Vererbung und Verteilung des Geschlechtes bei den höheren Pflanzen. In: E. BAUR and M. HARTMAN (e.d.), Handbuch der Vererbungwissenschaft 2 C: 29–40, 124–125. Berlin.

CORTESI, R. (1943). Contribution à l'anatomie des pétioles des *Acer*. Bull. Soc. Bot. Suisse **53**: 102–113.

CRAIB, W. G. (1920). Contributions to the flora of Siam. Kew Bull. 1920: 301–302.

CRITCHFIELD, W. B. (1971). Shoot growth and heterophylly in *Acer*. J. Arn. Arb. **52**, 2, 240–266.

CROIZAT, L. (1952). Manual of phytogeography or an account of plant dispersal throughont the world. The Hague, the Netherlands, 558 pp.

DANSEREAU, P. and Y. DESMARAIS (1947). Introgression in sugar maples II. Amer. Midl. Nat. **37**: 146–161.

DANSEREAU, P. and A. LAFOND (1941). Introgression des caractères de l'*Acer saccharophorum* K. Koch et de l'*Acer nigrum* Mich. Centr. Inst. Bot. Univ. Montreal 37: 17–31.

DARWIN, C. (1877). Die verschiedenen Blüthenformen an Pflanzen der nämlichen Art. Stuttgart. 304 pp.

DAYTON, W. A. (1945). A tricarpellary maple. Proc. Biol. Soc. Washington **58**: 27–28.

DE CANDOLLE, A. P. (1824). Prodromus systematis naturalis regni vegetabilis **1**: 593–596. Paris.

DE MAGGIO, A. E. and J. A. FREEBERG (1969). Dormancy regulation: hormonal interaction in maple (*Acer platanoides*). Can J. Bot., **47**: 1165–1169.

DENKOVSKI, R. (1973). [Neue Beitrage zur Kenntnis die Arten *Acer campestre* L. und *Acer marsicum* Guss.] Godisen Zbornik, Biol. (Skopje) **25**: 185–203.

DENKOVSKI, R. (1974). *Acer marsicum* Gussone in der Flora Bulgariens. Godisen Zbornik, Biol. (Skopje) **26**: 221–224.

DESCHÊNES, J. M. (1970). The history of the genus *Acer*, a review. Natur. Can. **97**: 51–59.

DESMARAIS, Y. (1947). Taxonomy of the sugar maples. Amer. J. Bot., **34**: 606.

DESMARAIS, Y. (1952). Dynamics of leaf variation in the sugar maples. Brittonia **7**, 5: 347–387.

DESMARAIS, Y. (1953). Taxonomy of the sugar maples. Amer J. Bot. **34**: 606.

DON, G. (1831). A general history of dichlamydeous plants. I: 647. London.

DRUDE, C. G. O. (1887). In: A. SCHENK, Handbuch der Botanik 3,2: 390. Breslau.

DUFFIELD, J. W. (1943). Polyploidy in *Acer rubrum* L. Chron. Bot. **7**, 8: 390–391.

EICHLER, A. W. (1875). Blühtendragramme. I: 350–354. Leipzig.

ELLIS, W. H. (1964). Revision of *Acer* Section *Rubra* in Eastern America, excluding *Acer saccharinum* L. Diss. abstr. **25**, 2:774.

ENDLICHER, S. L. (1836–1840). Genera plantarum secundum ordines naturales disposita. clas. no. **53**: 1055. Wien.

ERRICO, P. (1957). Studio sistematico delle entita italiane di '*Acer opalus* Mill'. Webbia **12**: 41–120.

FAEGRI, K. and L. VAN DER PIJL (1966). The principles of pollination ecology. Pergamon Press, New York. 248 pp.

FANG, W. P. (1939). A monograph of Chinese *Aceraceae*. Contr. Biol. Lab. Sci. Soc. China, Nanking. Bot. Ser. **11**, 1-9: 1–346.

FANG, W. P. (1966). Revisio taxorum *aceracearum* sinicarum. Acta Phytotax. Sin., Peking **11**, 2: 139–184.

FOSTER, C. (1933). Chromosome number in *Acer* and *Staphylea*. J. Arnold Arb. **14**: 386–393.

FOWDEN, L. and M. M. PRATT (1973). Cyclopropylamino acids of the genus *Acer*: distribution and biosynthesis. Phytochemistry **12**: 1677–1681.

FRASER, C. G. (1912). Induced hermaphroditism in *Acer negundo* L. Torreya, **12**, 6: 121–124.

FRYXELL, P. A. (1957). Mode of reproduction of higher plants. Bot. Rev., **23**, 3: 135–233.

GABRIEL, W. J. (1966). Onset and duration of stigma receptivity in sugar maple flowers. For. Sci. **12**: 14–18.

GABRIEL, W. J. (1962). Inbreeding experiments in sugar maple (*Acer saccharum* Marsh.) – Early results. Proc. 9th Northeastern For. Tree Improvement Conf.: 8–12.

GABRIEL, W. J. (1967). Reproductive behaviour in sugar maple: self-compatibility, cross-compatibility, agamospermy and agamocarpy. Silvae Genet., **16**, 5-6: 165–168.

GABRIEL, W. J. (1968). Dichogamy in *Acer saccharum*. Bot. Gaz. **129**: 334–338.

GAGNEPAIN, F. (1950). *Acéracées*. Supplement à la Flore Générale de l'Indo-Chine **1**, 9: 1003–1013. Paris.

GAMS, M. (1925). Fam. *Aceraceae*. Ahorngewächse. In: G. HEGI. Illustrierte Flora von Mittel-Europa, **5**: 262–295. München.

Gershoy, A. and W. J. Gabriel (1961). A technique for germinating pollen of sugar maple. J. For. **59**: 210.

Gray, A. (1858). Introduction to structural and systematic botany, e.d. **5**: 410. New York, Chicago.

Guard, A. T. and N. F. Anderson (1964). A comparative study of the vegetative transitional and floral apex of *Acer pseudoplatanus*. Amer. J. Bot. **51**: 675.

Haas, Th. P. (1933). Untersuchungen an der Gattung *Acer*. Ludwig Maximilians Universität (thesis), München, 45 pp.

Haasis, F. W. (1963). Polycarpellate fruits in bigleaf maple. Leafl. West. Bot. **10**: 29.

Hall, B. A. (1951). The floral anatomy of the genus *Acer*. Amer. J. Bot. **38**: 793–799.

Hall, B. A. (1954). Variability in the floral anatomy of *Acer negundo*. Amer. J. Bot. **41**: 529–532.

Hall, B. A. (1961). The floral anatomy of *Dipteronia*. Amer. J. Bot. **48**: 918–924.

Hall, B. A. (1967). Flower structure and breeding systems in the maples. The garden journal 1967: 84–89.

Hantke, R. (1965). Die fossilen Eichen und Ahorne aus der Molasse der Schweiz und von Oehningen (Süd Baden). Neujahrbl. Nat. Ges Zürich **167**: 1–108.

Hardin, J. W. (1956). Studies in the *Hippocastanaceae*, II. Inflorescens structure and distribution of perfect flowers. Amer. J. Bot. **43**: 418–424.

Hardin, J. W. (1957). A revision of the American *Hippocastanaceae* I and II Brittonia, **9**: 145–171; 173–195.

Haslam, E. (1965). Galloylesters in the *Aceraceae*. Phytochemistry, Oxford **4**: 495–498.

Hein, W. H. (1907) Some observations on the flowers of *Acer saccharinum*. Plant world **10**: 200–205.

Heine, E. W. (1966). Zur Kenntnis der Inhaltstoffe der *Aceraceae*. IV. Prüfung auf Saponine mit der Haemolyse test. Pharmazie **21**: 493.

Helmich, D. E. (1963). Pollen morphology in the maples (*Acer* L.) Papers Mich. Acad. Sci, A. and L. **48**: 151–164.

Heslop-Harrison, J. (1957). The experimental modification of sex expression in flowering plants. Biol. Rev. Cambridge Phil. Soc. **32**: 38–90.

Heslop-Harrison, J. (1972). Sexuality of *Angiosperms*. In F. C. Steward (ed.), Plant Physiology. A treatise VI C: 133–289.

Hoffmann, H. (1871). Zur Geslechtsbestimmung. Bot. Zeit. **29**: 81–89; 97–109.

Horaninov, P. (1847). Characteres essentiales. p. 182. Petropoli.

Hu, H. H. and W. C. Cheng (1948). New and noteworthy species of Chinese *Acer*. Bull. Fan Mem. Inst. Biol. n.s. **1**: 199–212.

Hutnik, R. J. and H. W. Yawney (1961). Silvical characteristics of Red Maple (*Acer rubrum*). Northeastern For. Exp. Stat., Stat. Pap. no. 142. 18 pp.

Irving, R. M. and F. O. Lanphear (1967). Dehardening and the dormant condition in *Acer* and *Viburnum*. Proc. Amer. Soc. Hort. Sci **91**: 699–705.

Jong, A. W. de and J. Bruinsma (1974a-c). Pistil development in *Cleome* flowers. I. Effects of nutrients and of the presence of leaves and fruits on female abortion in *Cleome spinosa* Jacq. Z. Pflanzenphysiol. **72**: 220–226. III. Effects of growth-regulating substances on flower buds of *Cleome iberidella* Welw. ex Oliv. grown in vitro. Ibid **72**: 227–236 iv. Effects of growth-regulating substances on female abortive in *Cleome spinosa* Jacq. I bid. **73**: 152–159.

Jong, P. C. de (1974). Esdoorns met een streepjes-bast. *Acer* L. Sectie *Macrantha* Pax. Groen, **30**: 104–107.

Joshi, A. C. (1939). A note on the determination of sex of Plantain flowers. J. Genetics **38**: 353–356.

Jussieu, A. L. de (1789). Genera plantarum (secundum ordines naturales disposita). ed. **1**: 250. Paris.

Kabulov, S. K. (1966). [Polycarpellate fruits of some species of maple (*Acer* L.)]. Bot. Žur. **51**: 1617–1620.

Keller, A. C. (1942). *Acer glabrum* and its varieties. Amer. Midl. Nat. **27**: 491–500.

KLAEHN, F. U. (1958). Some interesting aspects of flower morphology and flower ecology of various forest trees. Proc. 5th Northeastern For. Tree Improvement Conf.: 71-76.

KLAEHN, F. U. (1959). Flower morphology and flower ecology with respect to forest tree breeding procedures. Recent advances in botany. 1 × Int. Bot. Congr., Montreal. Univ. of Toronto Press, vol. 2 (sect. 14): 1666–1671.

KNUTH, P. (1904). Handbuch der Blütenbiologie II *Aceraceae* I: 216–218. Leipzig.

KOBENDZA, R. (1953). [Observations on the biology of the blossoming of the silvery maple (*Acer saccharinum L.*)]. Rocznik, Ann. Sect. Dendr. Soc. Bot. de Pologne **9**: 175–181.

KOCH, K. (1869). Dendrologie I: 518–545. Erlangen.

KOIDZUMI, G. (1911a) Revisio *Aceracearum* Japonicarum. J. Coll. Sci. Imp. Univ. Tokyo **32**: 1–75.

KOIDZUMI, G. (1911b) Observations on the *Aceraceae*. Bot. Mag. (Tokyo) **25**: 42–61 and 96–113.

KRAUSEL, R. and H. WEYLAND (1959). Kritische Untersuchungen zur Kutikularanalyse tertiärer Blätter IV. Palaeontographica B 105: 102–122.

KRIEBEL, M. B. (1957). Patterns of genetic variation in sugar maple. Ohio Agric. Exp. Stat. Bull. no. 791. 55 pp.

KRÜSSMANN, G. (1960). Handbuch der Laubgehölze, I: 87–127. Berlin and Hamburg.

LARSEN, P. R. (1958). Effect of gibberellic acid on forcing hardwood cuttings for pollencollection. Techn. Note Lake St. For. Exp. Stat., no. 538. 2 pp.

LAUTH, T. (1781). De *Acere*. Strassbourg. 40 pp.

LEENHOUTS, P. W. (1967). A conspectus of the genus *Allophyllus* (*Sapindaceae*). The problem of the complex species. Blumea **15**: 301-358.

LEENHOUTS, P. W. (1969). Florae Malesianae praecursores L. A revision of *Lepisanthes* (*Sapindaceae*). Blumea **17**, 1: 33–91.

LEIKE, M. (1967). Wirkung von Gibberellinsäure un Kinetin auf ruhende Knospen verschiedener Gehölze. Flora, Abt. A. Phys. Biochem. (Jena) **158**: 351–362.

LEINFELNER, W. (1955). Beiträge zur Kronblatt-morphologie, V. Über den homologen Bau der Kronblattspreite und der Staubblattanthere bei *Koelreuteria paniculata*. Österr. Bot. Z. **102**: 89–98.

LEINFELNER, W. (1958). Über die peltaten Kronblätter der *Sapindaceen*. Österr. Bot. Z. **105**: 443–490.

LEMAIRE, C. A. (1864). *Acer pseudoplatanus* var. *Leopoldii*. Illustration Horticole, 11, planche 411. Gent.

LINDLEY, J. (1836). A natural system of botany, ed. 2: 81. London.

LINNÉ, C. VON (1737). Genera Plantarum, ed. 1: 112. Leiden.

LINNÉ, C. VON (1742). Genera Plantarum, ed. 2: 159 Leiden.

LINNÉ, C. VON (1754) Genera Plantarum, ed. 5: 474. Stockholm.

LINNÉ, C. VON (1753). Species Plantarum: 1054–1056. Stockholm.

LIPPOLD, H. (1968). Die europäischen Arten der Gattung *Acer* aus der Sektion *Platanoidea*. Wiss. Zeit. Univ. Jena, **17**: 341–347.

LIU, S. Y. (1954). Studies of *Litchi chinensis* Sonn. University of Michigan (thesis). 238 pp.

MACKENZIE, K. K. (1926a) *Acer saccharum* Marsh. Rhodora **28**: 111–112.

MACKENZIE, K. K. (1926b). Technical name of sugar maple. Rhodera **28**: 233–234.

MAC LEOD, J. (1894). Over de bevruchting der bloemen in het Kempisch gedeelte van Vlaanderen. 551. *Acer Pseudo-Platanus* L. Botanisch Jaarboek. Dodonaea **6**: 240.

MAXIMOWICZ, C. J. (1867). Diagnoses breves plantarum novarum Japoniae et Mandshuriae. VI. Bull. Acad. Imp. St. Petersbourg **12**: 225–228.

MAXIMOWICZ, C. J. (1880). Diagnoses plantarum novarum Asiaticarum. III. Bull. Acad. Imp. St. Petersbourg. **26**: 436–451.

MEEMAN, T. (1879a). Notes on *Acer rubrum*. Proc. Acad. Nat. Sci. Philadelphia 1878: 122–123.

MEEMAN, T. (1879b). The law governing sex. Ibid. 1879: 267–168.

MEEMAN, T. (1889, 1891). Contributions to the life-histories of plants. III. Dichogamy and its significance. Proc. Acad. Nat. Sci. Philadelphia 1888: 391–394. V. On the male and hermaphrodite flowers of *Aesculus parvflora*. Ibid. 1890: 274–275.

MEHRA, P. N., P. K. KHOSLA and T. S. SAREEN (1972). Cytogenetical studies of Himalayan *Aceraceae*, *Hippocastanaceae*, *Sapindaceae* and *Staphyleaceae*. Silvea Genet. **21**: 96–102.

MERRILL, E. D. (1932). A fourth supplementary list of Hainan plants Lignan Sci. Journ. **11**: 47.

MIQUEL, F. A. W. (1865). Prolusio Florae Japonicae. Ann. Mus. Bot. Ludg. Bot. **2**: 86–90.

MIQUEL, F. A. W. (1867). Sur les érables du Japon. Arch. Neerl. **2**: 467–480.

MOMOTANI, Y. (1961, 1962a, 1962b). Taxonomic study of the genus *Acer* with special reference to the seed proteins. I. Taxonomic characters. Kyoto Univ. Mem. Col. Sci. ser. B **28**: 455–470. II. Analysis of protein. Ibid. **29**: 81–102. III. System of *Aceraceae*. Ibid. **29**: 177–189.

MULLER, J. and P. W. LEENHOUTS (1976). A general survey of pollen types in *Sapindaceae* in relation to taxonomy. In: FERGUSON, I. K. and J. MULLER (eds.), The evolutionary significance of the exine. (Linn. Soc. Symp. Ser. No. 1). London & New York, Academic Press (in the press).

MURNEEK, A. E. (1927). Physiology of reproduction in horticultural plants. II. The physiological basis of intermittent sterility with special reference to the spider flower. Univ. of Missouri, Res. Bull. Missouri Agric. Exp. Stat. no. 106. 37 pp.

MURRAY, E. A. (1966). New combinations of Asiatic subspecies of *Acer*. Morris Arb. Bull. **17**: 51.

MURRAY, E. A. (1969, 1970). *Acer* notes. Nos. 1-6-Kalmia **1**: 1–42. No. 7. Kalmia **2**: 1.

MURRAY, E. A. (1970). A monograph of the *Aceraceae*. The Pennsylvania State University (thesis). Ann Arbor, Michigan. 332 pp.

MURRAY, E. A. and K. H. RECHINGER (1969). *Aceraceae*. Flora Iranica **61**: 1–11. Wien.

MUSHEGIAN, A. M. (1953). [The silver maple in Alma-Ata]. Bull. Glav. Bot. Sada **19**: 128–129.

MUSTARD, M. J., S. Y. LIU and R. O. NELSON (1954). Observations on floral biology and fruit-setting in Lychee varieties. Proc. Florida Hort. Soc. **66**: 212–220.

NAKAI, T. (1915a). Flora sylvatica Koreana. *Aceraceae*. **1**, 1: 1–23.

NAKAI, T. (1915b). Praecursores ad Floram Sylvaticam Koreanum. I. Bot. Mag. (Tokyo), **29**: 25–30.

NAPP-ZINN, K. (1967). Modifikative Geschlechtsbestimmung bei Spermatophyten. In: W. RUHLAND (Ed.) Handbuch der Pflanzenphysiologie 18, Berlin-Heidelberg-New York p. 153–213.

NEILREICH, A. (1846). Flora von Wien: 565. Wien.

NICHOLSON, G. (1881). The Kew Arboretum. The Maples I-XVI. Gard. Chron., N.s. **15**: 10, 42, 74–75, 137–136, 141, 172–173, 268, 299–300, 364–365, 499, 532–533, 564–565, 725–726, 788; Ibid. 16: 75, 136–137, 375–376, 590–591, 719, 750–751, 815.

NIEUWLAND, J. A. A. (1911). Box-elders, real and so-called, Amer. Midl. Nat. **2**: 129–142.

NIEUWLAND, J. A. A. (1914). Critical notes on new and old genera of plants. I. Amer. Midl. Nat. **3**: 181–183.

NITSCH, J. P. and C. NITSCH. (1965). Présence de phytokinines et autres substances de croissance dans la sève d'*Acer saccharum* et de *Vitis vinifera*. Bull. Soc. Bot. France, **112**: 11–18.

OGATA, K. (1965). A dendrological study on the Japanese *Aceraceae*, with special reference to the geographical distribution. Bull. of the Tokyo Univ. For. **60**: 1–99.

OGATA, K. (1967). A systematic study of the genus *Acer*. Bull. of the Tokyo Univ. For. **63**: 89–206.

PARKIN, J. (1953). The Durian theory – a criticism. Phytomorphology **3**: 80–88.

PAX, F. (1885, 1886). Monographie der Gattung *Acer*. Bot. Jahrb. **6**: 287–374; Ibid. **7**: 177–263.

PAX, F. (1902). *Aceraceae*. In: A. ENGLER, Das Pflanzenreich IV, 163, **8**: 1–89.

PAX, F. (1926, 1927). In: E. HANNIG and H. WINKLER (ed.), Die Pflanzenareale **1**; 1, 2 Karte 4–5 und 4, Karte 31–33. Jena.

PAYER, J. B. (1857). Traité d'organogène végétale comparée de la fleur: tab. 27. Paris.

PITCHER, J. A. (1960). Heteroplastic grafting in the genera *Acer, Fraxinus, Picea* and *Abies*. Proc. 7th Northeastern For. Tree Impr. Conf., Aug. 18–19, 1959, Burlington, Vermont: 52–58.

PLOWMAN, A. B. (1915). Is the box elder a maple? A study of the comparative anatomy of *Negundo*. Bot. Gaz. **60**: 169–192.

POHL, F. (1937). Die Pollenerzeugung der Windblülter. Eine vergleichende Untersuchung mit Ausblicken auf den Bestaubungshaushalt tierblütiger Gewächse und die pollenanalytische Waldgeschichtsforschung. Beih. Bot. Zbl. **56**: 365–470.

POJARKOVA, A. I. (1933). Botanico-geographical survey of the maples in USSR in connection with the history of the whole genus *Acer* L. Acta Inst. Bot. Acad. Sci. USSR, ser. **1**, 1: 143–155, 225–374.

POJARKOVA, A. I. (1949). *Aceraceae*. In KOMAROV, Flora USSR **14**: 580–622, 746.

POWERS, H. O. (1967). A blade tissue study of forty seven species and varieties of *Aceraceae*. Amer. Midl. Nat. **78**: 301–323.

RAFINESQUE, C. S. (1833). Florula Texensis. Atlantic Journ. **6**: 176.

RAFINESQUE, C. S. (1836). New Flora of North America, I, 47–49. Philadelphia.

RATIV, F. (1960). Un cas teratologic la fructul de *Acer negundo* L. Contr. Bot. Univ. Babes Bolvai diu Cluj Grad. Bot. (quotation KABULOV, *1966*).

REHDER, A. (1905, 1907) The maples of eastern continental Asia. In: SARGENT, C., Trees and Shrubs **1**: 131–181; ibid. **2**: 25–27.

REHDER, A. (1927). Manual of cultivated trees and shrubs. ed, **1**: 558–578. New York.

REHDER, A. (1933). New species, varieties and combinations. *Acer* sect. *Macrantha* Pax, emend. Rehd. J. Arnold Arb. **14**: 211–222.

REHDER, A. (1949). Bibliography of cultivated trees and shrubs: 412–429. Jamaica Plain.

REHDER, A. (1960). Manual of cultivated trees and shrubs, ed. 2: 565–586. New York.

REICHENBACH, H. G. L. (1828). Conspectus Regni Vegatabilis. Leipzig. 201 pp.

RECHENBACH, M. G. L. (1834). Das Pflanzenreich in seinen natürlichen Klassen und Familien entwickelt. Leipzig. 55 pp.

RIOU, P. and G. DELORME (1940). Natur. Can. **67**: 87 (quotation TOWERS and GIBBS, 1953).

ROUSSEAU, J. (1940). Histoire de la nomenclature de l'*Acer saccharophorum* K. Koch (*A. saccharum* Marshall). Natur. Can. **67**: 161–224.

SANTAMOUR, F. S. (1962). Chromosome number in striped and mountain maples. Rhodora **64**: 281–282.

SANTAMOUR, F. S. (1965). Cytological studies in red and silver maples and their hybrids. Bull. Torrey Bot. Club, **92**: 127–134.

SANTAMOUR, F. S. (1971). In: LÖVE, A., IOPB chromosome number reports. Taxon **20**: 355.

SARGENT, C. S. (1891, 1902). Silva of North America **2**: 79–113; ibid. **13**: 7–11. Boston.

SARGENT, C. S. (1905). Manual of the trees of North America: 624–643. Boston and New York.

SCHNEIDER, C. K. (1907, 1909). Illustriertes Handbuch der Laubholzkunde, **2**: 192–240; ibid. **2**: 241–245. Jena.

SCHOLZ, E. (1960). Blütenmorphologische und biologische Untersuchungen bei *Acer pseudoplatanus* L. und *Acer platanoides* L. Der Züchter **30**, 1: 11–16.

SCHUEPP, O. (1929). Untersuchungen zur verschreibenden und experimentellen Entwicklungsgeschichte von *Acer pseudoplatanus* L. Jahrb. Wiss. Bot. **70**: 743–804.

SCHWERIN, F. VON (1893). Die Varietäten der Gattung *Acer*. Gartenflora **42**: 161–168; 200–205; 228–233; 258–269; 324–329; 359–365; 454–460; 559–563–650–654; 678–683; 708–714.

SCHWERIN, F. VON (1903). *Acer* In: BEISSNER, SCHELLE und ZABEL, Handbuch der Laubholz-Benennung: 297–320. Berlin.

SEMBDER, G. c.s. (1968). Isolation, structure and metabolism of gibberellin glucoside. Plant grow regulator. S.C.I. Monograph **31**: 70–86.

SIMSÍKOVÁ, J. (1969). [A new method to break dormancy of terminal buds of *Acer pseudoplatanus* L.]. Acta Univ. Palackianae Olomuc. Fac. Rer. Nat. **31**: 49–56.

SMALL, J. K. (1933). Manual of the southeastern flora, 823–826. Chapel Hill.

SMITH, W. W. (1917). Diagnoses Specium Novarum. Notes Roy. Bot. Gard. Edinburgh **10**: 329.

SPACH, E. (1834). Revisio generis *Acerum*. Ann. Sci. Nat. Bot. ser. 2, **2**: 160–180.

SPÄTH, H. L. (1912). Der Joannistrieb. Berlin. 91 pp.

SRAGUE, T. A. (1929). The botanical name of the sugar maple. Kew Bull. 1929: 81–82.

STAFLEU, F. A. (ed.) (1972). International code of botanical nomenclature. Utrecht. 426 pp.

STARITSKY, G. (1970). The morphogenesis of the inflorescences, flower and fruit of *Pyrus nivalis* Jacquin var. *orientalis* Terpó. Meded. Landbouwhogeschool Wageningen **70**, 5: 1–91.

STEBBINS, G. L. (1947). Rates of evolution of fossil plant species. Ecol. Monog. **17**: 149–158 (quotation DESCHÊNES, 1970).

STEBBINS, G. L. (1951). Natural selection and the differentiation of *angiosperm* families. Evolution **5**: 299–324.

STOUT, A. B. (1928). Dichogamy in flowering plants. Bull. Torrey Bot. Club **55**: 141–153.

STOUT, A. B. (1938). The flowering behaviour of Norway maples. Journ. New York Bot. Gard. **39**: 130–134.

SUDWORTH, G. B. (1926). Technical name of the sugar maple. Rhodora **28**: 179.

SVOBODOVÁ, D. (1972). [Flower ecology and cultivars of the Norway maple (*Acer platanoides* L.)]. Acta Mus. Silesiae ser. C Dendrol. **2**: 163–169.

SVOBODOVÁ, D. (1973). Subspezifische Taxone von *Acer platanoides* und ihre Blütenbiologie. In: F. BENČAT. International Symposium on Biology of Woody Plants (Nitra, May 10th–17th, 1967): 49–54. Bratislava.

SYTSEMA, W. (1962). Bloei van sering aan afgesneden takken. Meded. Landbouwhogeschool, Wageningen. **62**: 2: 1–57.

TAYLOR, W. R. (1920). A morphological and cytological study of reproduction in the genus *Acer*. Contr. Bot. Lab. Univ. Penn. **5**, 2: 112–138.

THOMPSON, R. C. (1968). Regulation of the cataphyll-foliage leaf transition in sugar maple. Diss. Abstr. **29** B, 8: 2778.

THORNE, R. F. (1963). Some problems and guiding principles of *angiosperm* phylogeny. Amer. Natur. **97**: 287–305.

THUNBERG, C. P. (1784). Flora Japonica: 160–163. Leipzig.

THUNBERG, C. P. (1793). Dissertatio botanica de *Acere*. Uppsala. 12 pp.

TIEDJENS, V. A. Sex ratios in cucumber flowers as affected by different conditions of soil and light. J. Agric. Res. **36**: 721–746.

TOURNEFORT, J. P. DE (1703). Corollarium institutionum rei herbariae: 43. Paris.

TOWERS, G. H. N. and R. D. GIBBS (1953). Lignin chemistry and the taxonomy of higher plants. Nature **172**: 25–26.

TROLL, W. (1935). Vergleichende Morphologie der Fiederblätter. Nova Acta Leop. Carol. N.F. **2**: 315–455.

TROLL, W. (1964). Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskörpers. **1**: 108–111. Stuttgart.

TURRILL, W. B. (1962). *Acer nikoense*; *Aceraceae*. Curtis Bot. Mag. **173**: tab. 387.

ULBRICH, E. (1928). Biologie der Früchte und Samen.

VOGLER, P. (1906). Kleine botanische Beobachtungen. 1. Der Verlauf des Blühens von *Acer platanoides* L. im Stadtspark St. Gallen. Jahrb. St. Galler Naturw. Ges. 1905: 343–353.

WAHLENBERG, G. (1820). Flora Upsaliensis: 339–340. Uppsala.

WALTER, H. (1972). Studien über tertiäre *Acer* Mitteleuropas. Abh. Staatl. Mus. Mineral. Geol. **19**: 1–309.

WALTERS, S. M. (1968). *Aceraceae* in T.G. TUTIN, c.s. (ed.) Flora Europaea **2**: 237–239. Cambridge.

WARSOW, G. (1903). Systematisch-anatomische Untersuchungen des Blattes bei der Gattung *Acer* mit besonderer Berücksichtigung des Milchsaftelemente. Beih. Bot. Centralbl. **15**: 493–601.

WATARI, S. (1936). Anatomical studies on the vascular system in the petioles of some species of *Acer*, with notes of the external morphological features. Journ. Fac. Sci. Univ. Tokyo, sect. 3, **5**: 1–73.

WEISER, F. (1973). Betrag zur Klärung Blütenbiologischer Fragen bei *Acer pseudoplatanus* L. In: F. BENČAT (ed.). International symposium on biology of woody plants (Nitra, May 10th–17th, 1967): 83–88. Bratislava.

WESMAEL, A. (1890). Revue critique des espèces du genre *Acer*. Bull. Soc. Roy. Belgique **29**: 17–65.

WINCH, F. E. and R. R. MORROW (1962). Production of maple sirup and other maple products. Cornell Extension Bull. no. 974. 40 pp.

WITTROCK, V. B. (1886). Uber die Geschlecterverteilung bei *Acer platanoides* L. und einige anderen *Acer*-Arten. Bot. Centralblat. **25**: 2, 55–68.

WRIGHT, J. W. (1953a). Summary of tree-breeding experiments by the Northeastern Forest Experiment Station 1947–1950. Stat. Pap. Northeast For. Exp. Stat. no. 56: 8–15.

WRIGHT, J. W. (1953b). Notes on the flowering of northeastern trees. Stat. Pap. Northeast For. Exp. Stat. no. 60. 38 pp.

WRIGHT, J. W. (1957). New chromosome numbers in *Acer* and *Fraxinus*. Morris Arb. Bull. **8**: 33–34.

WYDLER, (1857). Flora: 27 (quotation PAX, 1885).

YALTIRIK, F. (1967). *Aceraceae*. In P. H. DAVIS (ed.), Flora of Turkey **2**: 509–519. Edinburgh.

YAMPOLSKI, C. and H. YAMPOLSKI (1922). Distribution of sex forms in the phanerogamic flora. Bibl. genet. **3**: 1–62.

ZELLER, O. (1955). Entwicklungsverlauf der Infloreszenzknospen einiger Kern- und Steinobstsorten. Angew. Bot. **29**: 69–89.

ZELLER, O. (1960). Entwicklungsgeschichte der Blütenknospen und Fruchtanlagen an einjährigen Langtrieben von Apfelbüschen I. Entwicklungsverlauf und Entwicklungsmorphologie der Blüten am einjährigen Langtrieb. Zeitschr. für Pflanzenzüchtung **44**, 2: 175–214.

ZIEGENFUS, T. T. and R. B. CLARKSON (1971). A comparison of the soluble seed proteins of certain *Acer* species. Can. J. Bot. **49**: 11, 1951–1957.

SPECIMENS EXAMINED

The list below does not concern all the studied herbarium specimens. It includes type-collections, specimens mainly studied for sex expression, loans and the collections at Wageningen. The following collections were studied: British Museum (Natural History) (BM), Royal Botanic Garden (E), Kew Herbarium (K), Rijksherbarium (L), Laboratoire de Phanérogamie (P), Botanisch Museum (U), Naturhistorisches Museum (W) (see pag. 29).

The collections at Wageningen mainly concern cultivated plants. The most important collectors are abbreviated: B = Boom (collection at L with duplicates at the Institute for Horticultural Plant Breeding (WAHO)), BR = Bruyn & Steenbergen, partly Bruyn & Baud (numbers are garden numbers of Wag. B.G.), D = Doorenbos or Doorenbos & Doorenbos (collection unnumbered), J = de Jong (1–854 (WAG), 855–1195 (WAHO)), R = Ruisch (garden numbers Wag. B.G.), S = Springer (Herbarium Dendrologicum, unnumbered), V = Vrugtman or Vrugtman & Vrugtman (specimens partly from Wag. B.G.), VS = Valckenier Suringar (specimens unnumbered), W = A. P. Wilson (specimens unnumbered). With exception of Boom these collectors concern Herbarium Vadense (WAG).

In the case of more than one collector only the first collector is mentioned.

A. acuminatum Wallich ex. G. Don.
Wallich 1212 p.p. (K,P: paratype) Lace 1377, s.n. (E); Stachey 6 (P). *Culta*: B 40742; J 952-3, 1093.

A. aidzuense (Franchet) Nakai
Culta: J 11, 128, 364, spirit 117.

A. amplum Rehder
Ching 1466 (BM); Forrest 13655, 17908, 19345, 24394 (K); Wilson 1906 (K: isotype). *Culta:* B 32032, 32239; J 96, 249, 501, 594-5, 689, 846, 927; J spirit 217.

A. argutum Maxim.
Tschonoski s.n. (L, P; isotypes); Faurie 4121 (P, WAG); Kanai 9642 (WAG); Siebold s.n. (L) *Culta:* B 1741 (L), 38900; J 922, 593, 1123, 1130, 1178; V 75, s.n.

A. barbinerve Maxim.
Maximowicz s.n. (P, L; isotypes?); Palczevsky 363 a (BM). *Culta:* B 9252 (L), 40308; J 495, 1136; S; Van den Burgh s.n. (WAG); W.

A. buergerianum Miquel
Faurie 65 (P: isotype var. *formosanum* Hayata); Swinhoe 17693 (BM; holotype var. *ningpoense* Hance; K). *Culta:* B 30092, 32029, 39195; D; J 26, 57, 80, 104, 119, 120, 484, 596, 799, 813, 816; S; V 1747; VS.

A. caesium Wallich ex Brandis
Wallich s.n. (K: lectotype, isotypes) H. B. Calcutta s.n. (B.M); Clarke 29434 (BM); Collett 931 (K); Dobremez 35, 165 (BM); Duthie 11201, 13309 (BM); Forrest 5992 (K), 10047 (BM, K), 10074 (BM), 10274 (BM); Gamble s.n. (K); Kingdom Ward 10091 (BM); Ludlow 4393 (BM); Polunin 790, 56/244, 3925, 4189 (BM); Rock 25007 (K); Stachey 4 (BM); Shresltra 5029 (BM); Young s.n. (BM); Winterbottom 492 (K). *Culta*: B 27544; Caeshamp Castle s.n. (K); J 22, 1003, 1023, 1039, 1195; Ridgebourne s.n. (K).

A. campbellii Hooker f. & Thomson ex Hiern
Hooker s.n., Herb. Griffith 926 (K: lectotype; P: isotype); Hooker 110 (K); Hooker s.n. (L); Cane s.n. (K); Brillet s.n. (P); Clarke 26737A, 27565 (K); Delavay s.n. (P); Forrest 27267 (K); Gamble 1998A, 8021 (K); Hance 18622 (P); Hooker f. s.n. (P); Hara 7669 (K); Kermode 17243 (K); Kerr 21052 (P),; Kingdom Ward 8722 (K); Lister s.n. (P); Petelot 3767, 3870, 4231, 4233 (P); Shilling 396 (K); Tsai 54379. *Culta*: J 924, 965, 967, 986, 1005, 1011-3, 1022, 1129.

A. campestre L.

Anonymus 1607 (WAG); Alexander s.n. (WAG); Billot 948 (WAG); Bourgeau 350 (WAG); Gandoger s.n. (K); Halascy s.n. (K); Maly s.n. (K); Oertel s.n. (WAG); Szovitz s.n. (L); Willmott s.n. (K). *Culta*: BA; B 5999, 31715, 31718, 32302, 32964–5, 34387; Bakker 96 (WAG Braat 99 (WAG); J 10, 41, 166, 179, 270–1, 273, 289–291, 317, 326, 351, 368, 400, 415, 442–3, 512, 537, 568, 585, 597–8, 747, 784, 809, 942; Jeswiet 12 (WAG); Kok Akkersmit s.n. (WAG); Labohm s.n. (WAG); Meyer Drees 16, 243 (WAG); Mazzeo 2855 (WAG); 8; Sintenis 1729 (WAG); VS; Wiersma 56 (WAG); Winkler 4 (WAG); R 1742, 1766; J spirit 76–80, 85, 137, 141, 205, 226, 241, 249–50.

A. capillipes Maxim.

Tschonoski s.n. (BM, L, P,: isotypes); *Culta*: B 15341, 26806, 29572, 30555, 32037, 32461; D; J 223, 406, 419, 604–5, 754–5, 822–3, 842, 933, 958, 1018–9, 1054, 1169, 1176; S; V 1743; J spirit 102, 105, 220.

A. cappadocicum Gleditsch

Herb. Tournefort s.n. (P: holotype); Wilson 1009, 1884, 1903 (K); Maung 5318 (K). *Culta*: B 32261; Bruyn 2060 (WAG); Baas Becking s.n. (WAG); J 31, 60, 73, 168, 198, 301, 314, 352, 356, 377, 392, 403, 412, 486, 513, 599–603, 699, 815, 1049; Jeswiet s.n. (WAG); R 1776; S; Valchem s.n. (WAG); V 947, 1367; J spirit 81, 236.

A. carpinifolium Siebold & Zuccarini

Siebold s.n. (L: lectotype, paratypes), Kanai 9461 (WAG); Togashi 10628 (WAG). *Culta*: B 2239, 5971; J 158, 172, 254, 298–9, 355, 463–5, 502, 533, 711–6; BR 1772; R; S; J spirit 113, 201, 259.

A. catalpifolium Rehder

Wilson 3350 (K: isotype); Chien 5681 (P).

A. caudatifolium Hayata

Culta: J 935, 1004, 1015; Mulligan s.n. (WAG).

A. ceriferum Rehder

Wilson 1934 (BM, K: isotypes).

A. chapaense Gagnepain

Petelot 5824 (P: holotype), 8177 (P).

A. circinatum Pursh

Allen 115F (BM, K); Brown 529 (P); Burth-Davy 13/25F (K); Chandler 1283 (P); Dennis s.n. (U); Ehmer 2835 (P); Everdam s.n. (BM); Gray s.n. (P, WAG); Heller 3859H, s.n. (P); Herb. Hooker, s.n. (K); Howell sn.. (P); Lemmon 18 (P); Lunell s.n. (K); Lyall s.n. (K, P, U); Malte s.n. (BM); Mason 13284 (WAG); Moseley s.n. (K); Sandberg 624F (BM, K, P); Surksdorf 2745 (BM), s.n. (BM, P); Thompson 645, 4250, 6258 (K); Tracy 2997, 17294, 18424 (K), 3223 (U). *Culta*: BA; B 5535, 31855, 32468; J 21, 39, 42, 121, 157, 206–6, 211, 213, 726, 766, 1047, 1154; R 1759; S; VS; J spirit 110, 134, 244.

A. cissifolium (Siebold & Zuccarini) Koch

Siebold s.n. (L: holotype); Kanai 10376 (WAG). *Culta*: B 28426, 29415, 32960, 40309; BR 1763; D; Koehne 520 (WAG); R 1763; S; V 1404; VS; J spirit 107–8, 197.

A. confertifolium Merrill & Metcalf

Tsang 21407 (BM, K, P; isotypes).

A. cordatum Pax

Henry 7721 (K, P: isotypes); Ching 2268 (P);

A. coriaceifolium Leveillé

Cavalerie 3100 (E: holotype).

A. crassum Hu & Cheng

Wang 87087, (K: isotype), 88839 (K: paratype).

A. crataegifolium Siebold & Zuccarini

Siebold s.n. (L: lectotype); Tschonoski s.n. (BM); Maximowicz s.n. (BM); Bisset 1033, 1036–7, 1546 p.p., 1985 (BM); Murala 1575 (U); Shimuzu 7403 (U); Togashi (U). *Culta*: B 40751; J 479, 758, 859, 865, 964, 1091, 1168, 1170; VS; Vandenburgh s.n. (WAG); Kew Gardens 258/33 (K).

A. davidii Franchet

David s.n. (P: lectotype; P, WAG: isotypes), 834 (P, WAG); Cheng 942 (K); Delavay 1096 (P, WAG), 4447 (P); Farges 140 (P, WAG); Forrest 2126 (E), 10045 (E, K), 12437 (E), 22599 (K); Gressitt 1532 (E); Henry 5356 (K); Law 1303 (K); Mc Laren 190 (E); Soulie 1369 (P, WAG); Steward 2620 (K); Wilson 225 (BM, E), 299 (E,P), 1882 (P). *Culta*: B 27547, 32043; Baas Becking s.n. (WAG); J 16, 19, 20, 74, 77, 218, 444, 493, 607–11, 762–4, 833–6, 855–7, 918, 936, 938–9, 1057, 1063, 1099, 1100, 1103, 1166–7, 1173; Kew Gardens 525/38 (K); Mazzeo 11409 (WAG); J spirit 200.

A. diabolicum Blume ex Koch

Siebold s.n. (L: holotype); Aoki 926 (K); Kanai 10126–7 (WAG); Tschonoski s.n. (P). *Culta*: B 32529, 38898, 40059, 40274; Dudley 562 (WAG); J 52, 482, 926, 1043, 1104, 1125; W.

A. distylum Siebold & Zuccarini

Keiske 14 (L: lectotype); Bisset 3760 (BM); Faurie 1651 (P), 4280 (P, WAG); Koyama 2560 (BM); Maries s.n. (BM); Shimuzu s.n. (W); Sugawara s.n. (U); Takeda 15 (K); Togashi 9935 (WAG), Tschonoski (BM, K, L, P, W); Wilson 7002 (K). *Culta*: Jackson 61932 (BM), s.n. (BM); J 483, 1025, 1067, 1083, 1117, 1119, 1143–4, 1147.

A. divergens Koch ex Pax

Davis 30065 (BM). *Culta*: Kew Gardens 2 (K); J 68, 112, 496, 614, 826, 1066.

A. erianthum Schwerin

Henry 8989 (K, P: isotypes); Chu 2629 (BM); Farges s.n. (P, WAG); Pratt 342 (K); Wilson 2089 (K). *Culta*: Anonymus s.n. (K); J 24, 1002, 1033.

A. erythranthum Gagnepain

Poilane 23933 (P.: lectotype), 30049 (P; paratype); 18927, 6794 (P); Petelot 4227–9, 4232, 4414, 5060, 7900 (P).

A. fabri Hance

Faber 22220 (BM: isotype); Chun 43993 (P); Farges 1305 (P, WAG); How 73301 (P); Steward 851 (P); Tsang 21354 (P); Wang 89656 (K). *Culta*: J 929, 1102.

A. fenzelianum Handel-Mazzetti

Myotte s.n. (L); Petelot 5059, 5059b (P).

A. flabellatum Rehder

Henry 6900 (K, P: isotypes); Wilson 708, 1232 (K: paratypes); Chun 2466, 2521, 3152 (BM); 3285 (BM, P); Fang 2226 (P); Farges s.n. (P); Delavay s.n. (P); Forrest 11949 (K), 21797 (P), 24482 (K), 26503 (BM); Wang 23062 (P). *Culta*: J 1030, 1073, 1085, 1145, 1183, 1194.

A. forrestii Diels

Forrest 2106 (E: isotype), 2292 (E, P), 5602 (BM, E), 10063 (E), 14763 (E), 22009 (P), 22239 (E), 22380 (E), 28021 (E), 30463 (E), 30496 (E), 30726 (BM), 30949 (E); Maire 720 (E),; Rock 4149, 17993 (E); Schneider 1462 (E); Ten 548 (E). *Culta*: J 9, 143, 367, 532, 730, 934, 969–971, 980–1, 1055, 1092, 1157, 1163–4; J spirit 103–4, 139, 150.

A. fulvescens Rehder

Wilson 1004 (BM, K: isotypes). *Culta*: Woodward s.n. (K); J 932, 1064.

A. garrettii Craib

Garrett 77 (K: holotype; L: isotype); Tsang & Fung 253 (K: isotype *A. decandrum* Merrill); Anonymus 201630 (L); Chun 43433 (K, P); Fleury 30144 (P); How 72766 (P); Petelot 4795, 5969 (P); Poilane 10835 (P); Tsang 633 (K).

A. ginnala Maxim.

Fan 275 (L); Fang 10413 (BM), Wilson 1933 (BM). *Culta*: BA; B 32039, 32326; 32860, 40812; J 2, 28, 72, 78, 90, 101–2, 292, 339, 345, 348, 353, 359–361, 363, 365, 372, 401, 410–1, 476, 488, 517, 583, 801; Jeswiet s.n. (WAG); R; S; V 1309, 1851; W; J spirit 118, 135–6, 143, 147–8.

A. glabrum Torrey

Douglas s.n. (BM, K: isotypes *A. douglasii* Hooker); Allen 212 (K); Anonymus 1221 (P), 616 (BM), s.n. (K); Arséne 15749 (P); Baker 124, 672, 749, 1054 (K); Ball s.n. (K); Barret 3 (K); Beamish 8099 (WAG); Blankenship 105 (L); Brown 75 (P); Carter 4720 (K); Clokey

8017 (K, WAG); Copeland 423 (K); Culbertson 4554 (K); Cusich 1865 (P); Drushall 2802 (P); Duran 761, 3022 (P); Elmer 192 (P); Elrod s.n. (K;) Ewan 18532 (K); Farr s.n. (K); Fendler 101, 105 (L, K, P); Geyer s.n. (K); Goodling 186, 1173 (P); Gray s.n. (K); Greene s.n. (P); Hall 17, 83, 93, 96, s.n. (P); Hansen 811 (P); Hecate s.n. (K); Heller 3089 (P, L), 7043 (K), 11001 (K); Helmer 192 (P); Henry s.n. (K); Hitchcock 1518 (K); Howell s.n. (P); Jack 1290 (K),; Lyall s.n. (K, P); Machide 171 (P); Macoun 295, 297 (K); Mc Calla 2421 (K); Nelson 295 (K), 5786 (K, P), 7006 (K), 7387 (K, P); Nuttall s.n. (K); Pringle s.n. (P); Purpus 194, 1511 (P); Rehder 4720 (K); Rothrock s.n. (K); Sandberg 81 (K), 156 (K, P), 182 (K); Shan 145, 724 (P); Spalding s.n. (K); Tracy s.n. (K); Vasey 102 (P); Warren s.n. (K); Westwood 986 (K); Young s.n. (K) Zeller 992 (K). *Culta*: Kew Gardens 205 (K); J 485, 616, 818, 1037, 1131; V 57; S.

A. griseum (Franchet) Pax

Farges 955 (P: lectotype; P, WAG: isotypes); Wilson 340, 1883 (K), s.n. (L). *Culta*: B 32028, 32477, 44005; D; J 260, 440, 521, 554–5, 719, 767, 772, 778, 987, 1052; V 972; J spirit 188, 190, 227.

A. grosseri Pax

Chanet s.n. (P, WAG); Ching 2789 (E); Ducloux 2112 (P, WAG); Farges 140 (P); Hers 533 (P); Purdom 949 (E); Rock 15033 (E). *Culta*: B 11781, 26865, 27546, 28561, 28563, 28601, 31992, 32041, 32049, 43295; Dudley 16308 (WAG); J 7, 8, 63–8, 75–6, 79, 88, 93, 123, 137, 145, 148, 224, 233, 293, 309, 319, 366, 497, 523, 530–1, 567, 617, 647, 731–2, 735, 739, 735, 756, 759, 768–9, 829–831, 861–2, 937, 944, 949, 1017, 1058–9, 1115, 1171; W; Vandenburgh s.n. (WAG); J spirit 93–4, 97–8, 127, 186, 230, 257.

A. heldreichii Orphanides ex Boissier

Orphanides 409 (K, P, WAG: isotypes); Anonymus 2668 (K); Hannibal s.n. (P); Heldreich 2668 (P); Webb s.n. (WAG). *Culta*: B 5998 (L); BR 12279; J 43, 618–9, 946, 1031, 1174; R 1745; S; Turrill 564 (K); Kew Gardens 129–08/Späth (K), Dieck 265 (K); VS; J spirit 82.

A. henryi Pax

Henry 5644-B (K: isotype), 5644 (K: paratype), 5644-A (BM); Cheng 2319, 2417 (BM); Kang 1266 (K); Wilson 424, 424A, 548 (K). *Culta*: B 30346; D; J 242, 253, 469–472, 487, 702–5, 949, 871, 947, 985; J spirit 184, 237, 247, 258.

A. heptaphlebium Gagnepain

Brillet 4 (P: lectotype, isotype), 1, 2 (P: paratypes); Evrard 2007 (P: paratype); Petelot 3871 (P: paratype).

A. hookeri Miquel

Hooker 3 (U: lectotype; K, P, WAG: isotypes); Clarke 27510, 27757B (K); Kingdom Ward 8062 (K). *Culta*: J 955, 1064.

A. hyrcanum Fischer & Meyer

Bornmüller 2719 (BM); Hohenacker (WAG); Webb s.n. (WAG): *Culta*: BA; Haussknecht s.n. (WAG); J 620, 1086, 1111.

A. japonicum Thunberg

Okubo 9629 (WAG). *Culta*: B 26315, 27197, 27931–2, 31870, 32649, 39012, 43292; BR 12681; J 97, 146, 202, 230, 295, 395, 520, 558, 687–8, 866, 1041, 1071, 1140, 1184–8; R; S; Schneider 509–512; Mazzeo 2923; V 1559, 1789, J spirit 11–2.

A. laevigatum Wallich

Wallich 1223 (K: lectotype; K, P: isotypes); Herb. Griffith 931 (P); Cole s.n. (P); Faber 455 (P); Falconer 341 (P); Fang 1220, 1224, 1226; 2129–30 (P); Forrest 26555 (K); Gamble 2001 (K); Harsukh s.n. (P); Henry 5538 (P); Hooker s.n. (P); Osmaston s.n. (K); Parkinson 4981 (K); Stachey 2 (K); Wilson 574, 574A, 3346 (P). *Culta*: J 930, 1007, 1101.

A. lanceolatum Mollaird

Beauvais 174 (P: holotype, isotypes). *Culta*: J 926, 950.

A. laurinum Hasskarl

Anonymus 2092 (L); Beumée 2378 (WAG); Bünnemeyer 12374, 12407 (L); Conklin 79517 (L); Forman 106 (K, L); Jungh s.n. (L); Koorders 7259, 7267 (WAG); Kostermans 18532 (K, L); Lindberg s.n. (K); Merrill 3872 (P: isotype *A. phillipinum* Merrill); Sulit 7608, 9991 (L); Vriese s.n. (L).

A. leipoënse Fang & Soong
Chu 3380 (BM, K).

A. lobelii Tenore
Tenore s.n. (K, P). *Culta*: J 178, 215, 323, 478, 508–9, 589, 693–4, 745, 810, 1079, 1180; VS; J spirit 215, 246.

A. longipes Franchet ex Rehder
Farges s.n. (BM, K. P: isotypes).

A. machilifolium Hu & Cheng
Liu 1205 (K).

A. macrophyllum Pursh
Abrahams 11469 (BM); Allen 114 (BM, K); Anonymus s.n. (BM, K); Baker 389 (K), 2981 (K), s.n. (P); Bigelow s.n. (K); Biolettil s.n. (K); Brewer s.n. (K); Charter 1041 (K); Clokey 4995 (K, P); Coulter s.n. (K); Coville 1166 (K); Doorenbos s.n. (WAG); Douglas s.n. (BM, K); Elmer 2836 (K), 3179 (K, P);, 3830 (K, P); Epling s.n. (K); Ewan 10515 (K); Eyerdam 1340, s.n. (BM); Fletcher 146 (BM); Gray s.n. (K); Haasis 1164, 1264, 1264, 1364, 2864 (WAG); Hansen 182 (P); Hartweg 26 (K), 1673 (P); Heerdt 452, 484 (U); Heller 5111, 8451, s.n. (P); Hichborn s.n. (U); Howel s.n. (P); Hughes s.n. (U); Hutchinson 2408 (BM); Jones 3808 (BM, P);, 28943 (BM); Kado 9 (U); Lamb 1042 (K); Lemmon 2 (P); Lyall s.n. (K); Macoun 301 (K), 3415 (K), s.n. (B.M); Meyer 827 (BM); Oordt 1109 (U); Parks 24068, 24117 (K); Parry s.n. (BM); Pringle s.n. (P); Reed 102 (P); Rehder 126 (K); Rose 34073 (K); Sandberg 501 (BMO; s.n. (BM); Sweetser s.n. (K); Suksdorf s.n. (BM, P); Thompson 3999 (K); Tracy 10955 (U); Vasey 83 (K), 226 (BM), s.n. (K, P); Zeller 1122 (K). *Culta*: BA; B 877, 34855; BR; J 171, 195, 210, 121, 286, 354, 539, 590, 622, 723, 791, 939; R 1770, 1779; S; Venema s.n. (WAG); VS; J spirit 44–52, 73, 142, 202, 245.

A. mandshuricum Maxim.
Maximowicz s.n. (BM, K, W: isotypes); Wilson 5647, 10536 (K): Kozlow 14069, 14070 (W). *Culta*: B 40060; J 61, 749, 966, 1046; S; VS.

A. maximowiczianum Miquel
Maximowicz s.n. (L: holotype; Wilson 368, 638 (BM, K); Cheng 4124 (BM); Tschonoski (BM, K, WAG); Anonymus s.n. (K). *Culta*: BA; B 5004, 8442, 38901, 40065; D; J 1, 3, 164, 243–6, 258–9, 272, 314, 346, 371, 527, 623, 863–4, 1024, 1026, 1126, 1121; Mazzeo 91242 (WAG); V 1892; VS; W; Jack A3337 (K); Kew Gardens 173 NSE 387 (K); J spirit 122–3, 235, 248.

A. maximowiczii Pax
Henry 6857 (BM, E, P: isotypes); Potanin s.n. (E: isotype *A. urophyllum* Maxim.); Farges 399 (P); Rock 17993 (E); Wilson 229 (BM), 355 (BM), 1914 (E). *Culta*: J 47, 87, 111, 274, 621, 952, 1056, 1095–7.

A. metcalfii Rehder
To 12135 (BM, P: isotypes).

A. micranthum Siebold & Zuccarini
Siebold s.n. (L: lectotype, isotypes, paratypes); Hotta 14871 (P, U); Murata s.n. (U; Nakaike 15571 (WAG). *Culta*: B 40760; J 84–5, 91, 261–5, 333, 477, 518, 556–7, 785–7, 790, 811; V 1813; J spirit 99, 207, 222.

A. miyabei Maxim.
Liou 11997 (K: isotype *A. miaotaiense* Tsoong). *Culta*: B 27196, 38903; D; J 313, 346, 371, 623, 727, 863–4, 1024, 1026, 1121; S; V 967; J spirit 203, 253.

A. mono Maxim.
Maximowicz s.n. (K: isotype); Taguet 2790 (K: isotype var. *quelpaertense* Fang; T & Y 6681 (K); Faurie 1601 (BM, P); Maximowicz s.n. (K); Togashi 9946, 9947 (WAG: *Culta*: BA; B 32030, 40074, 40082, 38902; D; J 36, 51, 53, 153, 255, 378, 492, 504, 524, 624–5, 692, 848, 959, 1032, 1053, 1065, 1069, 1075, 1090, 1105, 1192; S; V 1097, 1780; VS; W; J spirit 216.

A. monspessulanum L.
Aleizette s.n. (L); Bach 26 (WAG); Balansa 971 (WAG); Bourgeau 203 (WAG); Brand s.n. (L); De Wilde 2615, s.n. (WAG); Facchini s.n. (WAG); Jacobs 6327, 6469, 6490 (L); Lagrèze-Fossat s.n. (WAG); Martini (WAG); Pette 3 (WAG); Segal 238 (WAG); Sauzé 1634 (WAG);

Salle s.n. (WAG); Touw 69 (WAG). *Culta*: B 29626, 31856; J 235, 237, 393, 511, 574–5, 727, 851; R 1744; S; VS; J spirit 255.

A. negundo L.

Baker 867 (K); Blake 9336 (K); Brewer 536 (K); Bijhouwer 190, 484 (WAG); Davis 2497 (K); Harmsen 22 (WAG); Meagher 98, 99 (WAG); Palmer 5908, 7546 (K); Roy 2886, 3073, s.n. (WAG); Summers s.n. (K); Schweinitz 1854 (K); Yamaguchi 1043 (WAG). *Culta*: BA; B 28666, 29185, 30418–9, 30453, 30592, 31651, 40067–9; BR 8310, 11471, 13166; J 126, 173, 175, 573, 580, 584, 728, 748, 757, 793, 795, 797, 803, 812; Mazzeo 993, 28080 (WAG); S; R 1764–5; V 1821, 1838, 1856, 1878; VS; J spirit 140, 149, 232, 239.

A. nipponicum Hara

Faurie 513 (K, P, W), 2311 (P, W), 2312 (P, WAG), 4418 (P), 5466 (BM, P, W), 6099 (BM, W); Okamoto 1309 (K, W); Takeda s.n. (K; Togashi 9957 (P); Shirasawa s.n. (K); Wanatobe s.n. (K); Wilson 7201 (BM, K); Yamazaki 9748 (K). *Culta*: B 32527; Baas Becking s.n. (WAG); J 98, 105, 252, 257, 474, 804, 845, 870; Balfour s.n. (K); Rechinger s.n. (W); J spirit 88, 189, 191–3.

A. oblongum Wallich ex Candolle

Wallich 1222 (K, P: isotypes): Dutta 688 (WAG); Farges 1333 (P). *Culta*: B s.n. (L); Bean s.n. (K); Kew Gardens 224 (K); J 627, 925, 1193.

A. oliverianum Pax

Henry 6512 (BM, K: isotypes), 6187 (K); Wilson 716 (K). *Culta*: B 32067; J 44, 103, 226, 238, 248, 481, 510, 628–9, 700, 943, 1038, 1116, 1124.

A. opalus Miller

Bavoux 2433 (WAG); Becking s.n. (WAG); Pedicino s.n. (WAG); Salle s.n. (WAG); Bourgeau s.n. (P); Huter 3 (P). *Culta*: BA; B 31857; J 17–8, 62, 83, 154, 194, 576, 578, 636, 657, 921, 1040, 1177; BR 2863, 12999, S; VS; V 1773, 1809, 1811, 1875, 1883, 1924; J spirit 96, 254.

A. osmastonii Gamble

Osmaston s.n. (K: lectotype, isotypes); Anonymus 396 (K); Kurz 1365. (P: isotype *A. isolobum* Kurz).

A. palmatum Thunberg

Kanai 10387 (WAG); Nakaike s.n. (WAG); Yamazaki 11036 (WAG). *Culta*: B 27917–28, 27198, 27930, 31869, 32467, 32469, 35037, 35186, 36106, 39508, 40081; BR 12254; Jansen s.n. (WAG); J 38, 49, 55, 94, 140, 144, 147, 177, 181, 184, 186, 199–201, 203–5, 228–9, 231–2, 239, 276–81, 283–5, 294, 296–7, 310, 379, 381, 388–9, 404, 413, 515, 529, 631, 670–86, 724, 729, 741, 853; Mazzeo 2046, 2843, 2851, 2904, 28022, 102293 (WAG); S; Schneider 501–8, 516–7, 519–26, 528–32, 534–5; R 1739; V 528, 411, 931, 973, 1397, 1560–3, 1072, 1772, 1777, 1779, 1782, 1786, 1792–4, 1819–20, 1823, 1829, 1833, 1835, 1837, 1845, 1869, 1872, 1925; W; J spirit 243.

A. pauciflorum Fang

Ching 1790 (K, P: isotypes).

A. paxii Franchet

Delavay 1 (P: lectotype), 894 (P: paratype); Forrest 12418, 23455, 23509 (BM); Handel-Mazzetti 2459 (P); Ten s.n. (P).

A. pectinatum Wallich

Wallich 1226 (BM: lectotype); Gamble 9486 (L); King's Coll. s.n. (L); Thomson s.n. (L). *Culta*: J 1109, 1093.

A. pensylvanicum L.

Bijhouwer 83A ,498, 530 (WAG); Harmsen 6, 161–2 (WAG); Roy 3177, 4258; Marie-Victorin 46721. *Culta*: BA; Baas Becking s.n. (WAG); B 31807; J 6, 92, 100, 227, 234, 240–1; 256, 275, 312, 336, 370, 421, 427–31, 707–10, 850; Rosenstock s.n. (WAG); R 1761; VS; J spirit 100–1, 106, 138, 187, 195, 198.

A. pentaphyllum Diels

Rock 17819 (BM, K, P, W: isotypes). *Culta*: J 920, 1084.

A. pentapomicum Stewart ex Brandis

Stewart 541 (K: lectotype), 648 (K: paratype); Gapus 285 (P: lectotype *A. pubescens* Franchet), 286–7 (P: paratypes A. p.); Aitchison 850, 853 (BM, K); Barrett 215553, 21558 (K);

Bowes Lyon 607 (BM); Clarke 31430 (BM); Collett 63 (K); Csuasda 284 (BM); Dmany pasol 45, 115 (K); Duthie s.n. (K); Fedjenko s.n. (P); Frigorjev 62 (K); Mohd 137 (BM); Parker 2910 (W), s.n. (K); Regel s.n. (K, P); Stewart 2954 (K); Stainton 2658 (BM); Toppin 189 (K); Winterbottom 358 (K); Young s.n. (BM).

A. pilosum Maxim.

Purdom 337 (K: isotype (*A. stenolobum* Rehder); Licent 2064 (BM, P).

A. platanoides L.

Blonsk s.n. (WAG); Franqueville 1442 (WAG); Jacobs 323 (L); Kovatz s.n. (WAG); Labohm s.n. (WAG); Sibilski 84 (WAG); Thomas s.n. (WAG); Wirtgen s.n. (WAG). *Culta*: BA; B 2230, 8435, 14843 (L), 18298 (L), 25548 (L), 25696, 29954, 30566, 30601, 30603, 31690 (L), 32264, 32401 (L), 32404, 33857, 39804, 40061-3, 40066, 40071, 40770; BR 1774, 11454–5, 11457, 12041, 12075–6, 12116; J 12–3, 124, 130, 132, 159, 165, 183, 187–92, 196–7, 331–2, 334–5, 380, 390–1, 417, 489, 516, 522, 591, 632–4, 690, 721, 743–4, 746, 792; R 1774, 1751; S; VS; J spirit 53–72, 75, 89–90, 144– 5, 212–4. 228, 256.

A. pseudoplatanus L.

Blonski s.n. (WAG); Brandhorst 214 (WAG); Heldreich s.n. (WAG); Segal 581 (WAG); Varekamp 32 (WAG); Wierzbicki 2592 (WAG); Ziesché 971–2 (WAG). *Culta*: BA; B 13272–3, 26919, 28357, 28371, 28394, 28422, 29967, 30599, 32401, 32403, 33857 34895, 36343, 43976; BR 8385, 11460, 11474, 11714, 11717, 12118; Braat 118 (WAG); Bruyn 2058–9 (WAG); Dudley 2836, 9631 (WAG); Hessel 1023 (WAG); J 12–3, 124, 130, 132, 159, 165, 183, 187–92, 196–7, 331–2, 318, 320–1, 324, 328–30, 337–8, 341–4, 369, 373–6, 382–7, 396, 398–9, 402, 408–9, 422–5, 433–9, 441, 540–1, 722, 725, 737, 742, 781, 783; Meyer Drees 37, 614 (WAG); R 1769, 1772, 1777; S; V 869, 1092–3, 1372, 1380, 1392, 1414, 1770, 1785, 1785, 1802, 1804, 1808, 1816, 1824, 1827, 1842, 1846, 1850, 1857, 1862–3, 1877, 1884–7; J spirit 1–43, 74, 83–4, 146, 208–11, 231, 242, 260.

A. pseudosieboldianum (Pax) Komarov

Wilson 8500 (BM). *Culta*: B 32026, 40079; J 37, 635, 852; AA 109.20 (K); Dudley 90785 (WAG).

A. pycnanthum Koch

Keiske s.n. (L: isotype); Furuse 1012 (K, W); Wilson 6882 (K), 7729 (BM, K).

A. reticulatum Champion

Barthe s.n. (P); Chun 40008 (P); Hance 224 (BM, P); Wright 71 (P). *Culta*: J 919.

A. robustum Pax

Wilson 339, 1940

A. rubrum L.

Bijhouwer 85, 145, 165, 264, 336, 350, 406, 411; Drummond 53 (BM); Harmsen 3, 19, 163 (WAG); Marie-Victorin 43223, 44120, 44700, 45502 (WAG); Redmond 483 (P); Roy 3178 (WAG). *Culta*: BA; B 21656, 30429, 34385, 40080, 40741; BR 1757, 7909; D; Dudley 91522 (WAG); Gamble 30348, 30535 (K); J 125, 152, 156, 176, 222, 325, 327, 349, 405, 418, 525, 569–71, 577, 579, 581–2, 734, 770, 780, 802, 1126; R 1582, 1746, 1748, 1756–7; S; V 914, 1514, 1781, 1784, 1841, 1860, 1868; VS; J spirit 124–5, 128–33, 163–81.

A. rufinerve Siebold & Zuccarini

Faurie 3858, 4171 (P, WAG); Keiske s.n. (L: holotype); Fukuoka 1016 (U); Togasi 10007 (K); Togashi 44 (WAG). *Culta*: BA; B 29535, 32287, 40284, 44007; BR 11357; D; Dudley 91522 (WAG); J 86, 108, 122, 127, 133, 247, 503, 526, 637–9, 695–8, 738, 760–1; 824–5, 858, 945, 948, 1098, 1156; V 1784; J spirit 92, 95, 183, 238.

A. saccharinum L.

Burges 420 (WAG); Bijhouwer 493–4; Eggert s.n. (P); Godfrey 55807 (WAG); Jones 24022 (K); Kirk 302 (L); Marie-Victorin 45331 (WAG) Rolland Germain 43482 (WAG); Roy 3104, s.n. (WAG). *Culta*: BA; B 8430, 28112, 29296, 30169, 30452, 31692, 32402, 34382, 34386, 34865, 39494, 39805, 40056–7, 400073, 40078, 40734–5, 40806; Bowin 685 (WAG); Brand s.n. (L); Labohm s.n. (WAG); Mazzeo 995 (WAG); Pearce s.n. (K); Pelkwijk s.n. (WAG); R 1760; Staring 70 (WAG); V 1090, 1376, 1776, 1803, 1806, 1822, 1828, 1840, 1867, 1874, 1894, 1900; VS; Wiersma 69 (WAG); J spirit 126, 151–62, 225, 253.

A. saccharum Marshall
Michaux Herb. s.n. (P: holotype *A. nigrum* Michaux f.); Baker 6553 (P); Baldwin 5373 (K); Ball 328 (K); Bijhouwer 45, 86, 115 (WAG); Deam 17299 (K); Engelman s.n. (K), Fernald 7747 (K); Gattinger 497 (K); Gray s.n. (K); Harmsen 4, 166 (WAG); Heller s.n. (P); Jack 1122 (K); Kriebel 849, 850 (K); Lemmon 2650 (K); Marie-Victorin 2051, 40052 (WAP); Olney s.n. (K); Palmer 5925, 6104, 6310, 12654, 14985, 15177, 15270, 15475, 15563, 16479 (K); Pierson s.n. (P); Pringle s.n. (K); Raleigh s.n. (K); Rehder 5 (K); Roy 3172 (WAG), 4271 (K); Sartwell s.n. (K); Vasey s.n. (K); Vaugh 7866 (K, P). *Culta*: BA; B 40734–5; J 34, 40, 50, 99, 107, 150, 163, 209, 347, 358, 640, 656, 720, 1080–1, 1107, 1113–4, 1127, 1139, 1142; Kew gard. A389: 02 (K); R 1750; S; Spach s.n. (L); V 1081, 1891; VS; Westonbirt Arb. 2 (K); Wiersma 70 (WAG); J spirit 182.

A. semenovii Regel & Herder
Anonymus 308 (BM); Soloskokov 4482A, 4482B (BM). *Culta*: J 32, 35, 54, 58, 70–1, 217, 494, 615, 796, 860, 1082.

A. sempervirens L.
Chaubard s.n. (P); Cotte s.n. (L); Doorenbos s.n. (WAG); Gaillardot 696, (P). 15474 (BM); Guinier (P); Heldreich s.n. (WAG); Herb. Tournefort s.n. (P); *Culta*: Baenitz 1063 (L); Baas Becking s.n. (WAG); Alleizette 1493 (L); J 23, 56, 59, 81–2, 630, 805, 931, 1070, 1077: S; Schwerin 1067; Venema s.n. (WAG).

A. shirasawanum Koidzumi
Siebold s.n. (L); Takeda s.n. (K). *Culta*: B 27188, 32528; J 1050; S; Vandenburgh s.n. (WAG).

A. sieboldianum Miquel
Keiske 97 (L: holotype). *Culta*: BA; B 40070; Baas Becking s.n. (WAG); Nicholson s.n. (K); S; Vandenburgh s.n. (WAG); VS.

A. sikkimense Miquel
Hooker 4 (U: holotype, BM, K, P: isotypes); Hooker s.n. (K, P); Forrest 9759, 26233 (K); Herb. Hasefoot Haines 2587 (K); Herb. Griffith 930 (K); Herb. Treutler 226 (K); Petelot 8592 (P, WAG); *Culta*: Nicholson s.n. (K).

A. sinense Pax
Henry 5831 (BM, K, P: isotypes), 5641 (K); Ching 1411 (P); Ducloux 2209 (P); Farges s.n. (P); Fang 282 (P); Handel-Mazzetti 12393 (P); Maire s.n. (P); Myotte s.n. (L); Steward 670, 850 (P); Wilson 616 (P), 3345 (BM, P), 6100 (P). *Culta*: J 921, 954

A. spicatum Lam.
Anonymus 1417 (P), s.n. (K, P); Baldwin 5018 (K); Bartram 5018 (K); Beattie s.n. (K); Biltmore Herb. 118A (K); Blake s.n. (K); Braxer s.n. (K); Breteler 71 (WAG); Bijhouwer 84, 87, 528, 532, 637, 656 (WAG); Chalweis 4421 (K); Chevalier s.n. (P); Chinton 2 (P); Cosson s.n. (P); Cing-Mars 178 (L); Drushel 5074, 5808, 9312 (P); Drummond s.n. (K); Eury s.n. (P); Fernald 23 (P), 32 (K), 5830 (K); Fowler s.n. (P); Grays. n. (P); Harmsen 5, 111 (WAG); Kirk 304 (L); Lawrence 1141 (L); Macoun 302 (K); Marie-Victorin 9150 (P), 33062 (P), (WAG), 43886 (WAG); Matthew s.n. (P); Michaux s.n. (P); Pearson s.n. (P); Porter s.n. (K); Rafinesque s.n. (P); Rehder s.n. (K); Regel 113 (K); Richardson s.n. (K); Robinson 184 (P); Rolland Germain 6227 (K), 9150 (P); Roy 2289, s.n. (WAG); Schnette s.n. (K); Scoggan 7686, 8090 (K); Senn 945 (K); Small s.n. (L); Stauffer 5957 (WAG); Surksdorf s.n. (L); Torrey s.n. (P); Trail s.n. (K); Westra s.n. (WAG); Whiting 563 (K); Zomey s.n. (K); Zuzeh s.n. (L). *Culta*: BA, B 27956; Grabowski s.n. (WAG); J 5, 138, 362, 414, 771, 779, 832, 1087–8, 1120; S; VS W; J spirit 86–7.

A. stachyophyllum Hiern
Hooker f. s.n. (L, P: isotypes); Cave s.n. (E); Farges 140 (P); Forrest 21630 (P); Licent 5136 (P); Prain's Coll. 312 (P); Wilson 298, 3348 (P). *Culta*: B 32035; J 33, 46, 350, 643–4, 658, 736, 940, 968, 982, 999, 1000, 1006, 1044, 1074, 1089, 1133, 1138, 1146, 1149, 1172; Vandenburgh s.n. (WAG); V 1771; J spirit 121.

A. sterculiaceum Wallich
Wallich 1224 (K: lectotype, BM: isotype), 1227 (K: lectotype *A. villosum* Wallich, BM: isotype A. vill.); Henry 6456 (BM, P: isotypes *A. franchetii* Pax); Bowes Lyon 80 (BM); Chu 2506 (BM); Hooker s.n. (BM, L); Kermode 17215 (K); Ludlow 16072 (BM); Myotte s.n.

(L); Wilson 91 (P). *Culta*: 216, 498, 916, 983, 989, 1008–10, 1132, 1150–2.

A. sutchuenense Franchet

Farges 955B (P: lectotype, isotypes); Wilson 639 (K, P), 1931 (K).

A. sycopsoides Chun

Ching 5336 (K: isotype)

A. taronense Handel-Mazzetti

Forrest 2650 (K); Kermode 17007, 17211 (K); Kingdom Ward 6864, 6877 (K); *Culta*: J 972–4

A. tataricum L.

Culta: BA; B 32033, 32044, 43980; Hohenacker 439, 2591 (WAG); J 14, 89, 131, 167, 315, 397, 407, 490, 507, 586, 645–6, 820, 1035; R 795, 1780; S; V 998; VS; J spirit 115–6, 118, 196.

A. tegmentosum Maxim.

Maximowicz s.n. (BM, K, L: isotypes), s.n. (K); Anonymus s.n. (BM, P); Komarov 1053 (P); Palczevsky 3631 (BM); Sargent s.n. (K). Culta: J 750; Vandenburgh s.n. (WAG).

A. tenellum Pax

Henry 5612 (BM, K, P: isotypes), 5410 (K); Clarke s.n. (K). Culta: D.

A. thomsonii Miquel

Thomson s.n. (U: holotype, K: isotype); Herb Drake s.n. (P). *Culta*: 612, 928.

A. tibetense Fang

Kingdon Ward 10368 (BM: isotype)

A. tonkinense Lecomte

Bon 3330 (P: lectotype, P, WAG: isotypes); Wang 87137 (K: isotype *A. liquidambarifolium* Hu & Cheng), 87146 (K: paratype *A. liq.*); Hansen 11171 (L); Steward 152 (BM, K, P, W), 613 (BM, K, W).

A. trautvetteri Medwed.

Ardasenoff s.n. (P); Bautherus 232 (P); Davis 32255 (BM); Huynicwiecki (P). *Culta*: B 34384; D; J 106, 160, 269, 311, 426, 475, 506, 534, 773–4, 782, 806–7; S; VS.

A. triflorum Komarov

Komarov 1051 (K, P), s.n. (P); Faurie 471 (P); Wilson 9103, 10527 (K). *Culta:* B 40058; J 45, 220, 648, 751, 1068, 1122.

A. truncatum Bunge

Bunge s.n. (K, P: isotypes); Chiao 2440 (K); Bushell s.n. (P); Liu 337 (K); Wang 1411 (K). *Culta*: J 505, 649, 691, 701, 752, 798; Mazzeo 81, 18578 (WAG); Vandenburgh s.n. (WAG).

A. tschonoskii Maxim

Komarov 1054 (K, P: isotypes var. *rubripes* Komarov); Faurie 702 (P, WAG); Hotta 5 (P, U). *Culta*: J 221, 236, 1094, 1164.

A. turkestanicum Pax

Culta: J 651.

A. tutcheri Duthie

Tutcher 588 (K: holotype); Herb. Honkong 7158 (P); Merill 12516 (BM); To 12516 (P).

A. ukurunduense Trautvetter & Meyer

Wallich 1225 p.p (K, P: type *A. caudatum* Wallich); Azuma s.n. (U); Chu 2440 (BM); 2700 (P); 3284 (BM); 3287 (P); Dhwof 329 (E); Fang 2812, 4139 (P); Farges s.n. (P); Faurie 473 (P), 499 (BM), 706 (P), 4969 (P), 6101–2 (BM), Forrest 26882 (E); Hooker s.n. (P); Komarov 1048, s.n. (P); Kuznekow 3632B (BM); Ludlow 5523 (E); Maximowicz s.n. (BM, K, P); Potanin s.n. (P); Pratt 69 (BM, P); Rock 14785 (P); Soulie 1363 (P, WAG); Stainton 657 (E); Togasi 44 (L); Tschonoski s.n. (L, P); Uno 15276, 15301 (P); Volkova 3632A (BM); Wilson 3347 (P). *Culta*: AA 12473 (K); J 819; Kew Gardens 537 (K); Nicholson s.n. (K).

A. velutinum Boissier

Aucher-Eloy 4293 (BM, P: isotypes); Bornmüller 6532 (BM), 6534 (BM, K); Nlokosicwicz 50 (L). *Culta*: B 27858, 299962, 32686, 33917; J 15, 25, 27, 29, 587, 652–4, 808, 827–8, 1028–9; Kew Gardens s.n. (K); S; VS.

A. wardii W. W. Smith

Kermode 17241 (K); Kingdon Ward 6759 (K), 8215 (K); Forrest 21645 (E, P); Rock 18417 (P), 22218 (BM, K).

A. wilsonii Rehder
Wilson 303 (K, P: isotypes); Handel-Mazzetti 12074 (P); Steward 158 (BM); Tsiang 5205 (P). *Culta*: 655, 1135.

A. x zoeschense Pax
Culta: BA; B 28388, 28425, 30449, 30788, 34390; J 180, 394, 514, 519; S; V 1858, 1861, 1896; VS;

Dipteronia dyerana Henry
Henry 11352 (K: holotype).

D. sinensis Oliv.
Henry 5696 (K: holotype, P: isotype), 6506 (P); Chu 3349, 3750 (P); Anonymus 69696 (P); Farges 408 (P); Wilson 939 (P). *Culta*: D; J 95, 266–8, 588, 659, 800, 841, 957, 990, 1001, 1137.

Aesculus parviflora Walt.
Culta: J 550.

Koelreuteria paniculata Laxm.
Culta: J 551–2.