

*Belg. J. Bot.* **139** (2) : 139-152 (2006)

© 2006 Royal Botanical Society of Belgium

## INDIGENOUS SPECIES OF *CRATAEGUS* (ROSACEAE-MALOIDEAE) IN FLANDERS (BELGIUM). AN EXPLORATIVE MORPHOMETRIC STUDY

Leander DEPYPERE<sup>1,\*</sup>, Kristine VANDER MIJNSBRUGGE<sup>2</sup>, Katrien DE COCK<sup>2</sup>, Pieter VERSHELDE<sup>2</sup>,  
Paul QUATAERT<sup>2</sup>, Jos VAN SLYCKEN<sup>2</sup> and Paul GOETGHEBEUR<sup>1</sup>

<sup>1</sup> Ghent University, Department of Biology, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium

<sup>2</sup> Research Institute for Nature and Forest, Scientific Institute of the Flemish Government,  
Gaverstraat 4, B-9500 Geraardsbergen, Belgium

(\* Author for correspondence; e-mail: leander.depypere@ugent.be)

Received 9 May 2005; accepted 8 December 2005.

**ABSTRACT.** — The taxonomy of the five *Crataegus* taxa indigenous in Flanders was studied through a morphometric analysis. The applicability of the taxonomic treatments of Christensen, the botanical authority on *Crataegus* in Europe, was evaluated. Leaf and fruit characteristics were analysed for a total of 186 individuals. The results show that *C. monogyna* and *C. laevigata* can easily be differentiated. The putative hybrids *C. ×media*, *C. ×subsphaerica* and *C. ×macrocarpa* are more difficult to delineate. *C. ×media*, the putative hybrid between *C. monogyna* and *C. laevigata*, shows a remarkably large range and overlap with both parental species for most of the characters studied. This phenotypic variation could be due to a shift in morphological characters through several generations of backcrossing with the parental species.

Although *C. rhipidophylla* was not yet found in Flanders, populations of both putative hybrids with *C. monogyna* (*C. ×subsphaerica*) and *C. laevigata* (*C. ×macrocarpa*) were recently inventoried. The individuals identified as *C. ×subsphaerica* are hardly distinguishable from *C. monogyna*. Introgression with the *C. monogyna* parent may have obscured the diagnostic characters. Therefore, the presence of a typical population of *C. ×subsphaerica* in Flanders is questionable. On the contrary, the few individuals of *C. ×macrocarpa* form a distinct group.

**KEY WORDS.** — *Crataegus*, hybridisation, introgression, morphology, taxonomy.

### INTRODUCTION

Species of *Crataegus* (hawthorn) vary from small, polycormic shrubs to monocormic trees up to 10 m tall (CHRISTENSEN 1992: 8), often growing in large, dense thickets. *Crataegus* species generally favour sites with high light intensity. Only a few species, for example *Crataegus laevigata* (Poiret) DC. and *Crataegus rhipidophylla* GANDOGER (BYATT 1977, LIPPERT 1978, cited in

CHRISTENSEN 1992: 16) are more tolerant to shade and can survive easily in more or less continuous forest. Generally, species of *Crataegus* occur on moist, deep, fine-textured soils, often in hedges (for *Crataegus monogyna* see SPARKS & MARTIN 1999, JONES *et al.* 2001, CROXTON & SPARKS 2002), but also in thickets and old forest edges. As the dominant linear feature in the landscape, hedges have an important function as wildlife habitat in farmland (CROXTON & SPARKS 2002)

and hawthorn thickets provide both food and cover for wildlife (see KENNEDY & SOUTHWOOD 1984, OSBORNE 1984, MACDONALD & JOHNSTON 1995, SPARKS *et al.* 1996).

Species of *Crataegus* generally flower abundantly during late spring and early summer. Their open and unspecialised flowers are pollinated by flies, beetles, bees and occasionally by ants (DICKINSON 1985, CHRISTENSEN pers. obs., cited in CHRISTENSEN 1992: 16). They usually produce large numbers of fruits during late summer and autumn (CHRISTENSEN 1992: 16).

Depending on the interpretation of the species concept, the genus *Crataegus* (Rosaceae) contains between 150 and 1200 species, distributed mainly in temperate regions of the Northern Hemisphere (CHRISTENSEN 1992: 1). In northwestern Europe three species are indigenous: *Crataegus monogyna* Jacquin, *C. laevigata* and *C. rhipidophylla* (MAES & RÖVEKAMP 1999: 24).

It is assumed that introgressive hybridisation between the different species and successive backcrossing with one of the parental species has resulted in a large number of phenotypically intermediate forms (BYATT 1975). "The general attribution to *Crataegus* of taxonomic complexity has been endlessly repeated..." (PHIPPS & MUNIYAMMA 1980, PHIPPS *et al.* 2003), often referred to as 'the *Crataegus*-problem'. It is often difficult to reconstruct the phylogeny of taxa when hybridisation plays a role in their evolution (CHRISTENSEN 1992, ARNOLD 1997). The overlapping morphological characteristics increase the taxonomic complexity, resulting in conflicting classifications (e.g. CHRISTENSEN 1996). According to POJARKOVA (1939a), GLADKOVA (1968), BYATT (1975a, 1976a, b), and CHRISTENSEN (1982a, b, 1984, 1985, 1992, all cited in CHRISTENSEN 1992), hybridisation, introgression, and subsequent polyploidy play a major role in the evolution in the Old World. Furthermore, (facultative) apomixis may also be a factor.

According to CHRISTENSEN (1992: 3-4), the problems in European *Crataegus* are the result of a number of factors. First, the species are inherently variable. Second, hybridisation, introgression, and subsequent variable degrees of

polyploidy or apomixis may occur and blur the delineation between the species (see appendix in CHRISTENSEN 1992 for ploidy counts). Third, it is often difficult to obtain all the taxonomically important structures at a given time. Fourth, Old World botanists have described a large number of new species and nothotaxa, often based on very slight differences. DICKINSON & CAMPBELL (1991: 350) suggest likewise that taxonomic complexity in genera of the Maloideae consists most notably of the recognition of large numbers of very narrowly defined species.

Until now, nature conservation paid special attention to herbaceous plants, and in forestry only the economically important trees were studied. Until recently, the identification and distribution of woody shrubs, like *Rosa* spp. and *Crataegus* spp. in Flanders was no priority, which increases the need for a profound morphometric study. So far, no morphological study that aimed at distinguishing *Crataegus* taxa in Flanders within the complex as defined by CHRISTENSEN (1992) has been conducted. Furthermore, the conflicting results from the previous studies in Europe (see *Taxonomic history* in CHRISTENSEN 1992: 5-7) urged for a detailed morphological analysis of the *Crataegus* complex in Flanders.

Recent inventories of autochthonous trees and shrubs in Flanders (MAES & RÖVEKAMP 1998, MAES & RÖVEKAMP 1999, RÖVEKAMP *et al.* 2000, OPSTAELE 2001, MAES *et al.* 2003) have shed new light on the distribution and presence of possible autochthonous species. *C. monogyna* and *C. laevigata*, together with the hybrid taxa *C. ×media* (*C. monogyna* × *C. laevigata*), *C. ×subsphaerica* (*C. monogyna* × *C. rhipidophylla*) and *C. ×macrocarpa* (*C. laevigata* × *C. rhipidophylla*) are indigenous in Flanders (MAES & RÖVEKAMP 1999: 24). The inventories have been focussed on old woodlands, wood banks and ancient forests that are searched for following a set of criteria (MAES 1993).

*C. monogyna* is (very) common in Flanders, especially in old hedges and thickets (THOMAES & VANDER MIJNSBRUGGE 2001). In the past it was frequently planted in hedges to delineate field boundaries and to provide a barrier to grazing livestock. However, as a result of agricultural

intensification during recent decades with high animal stocking rates and concomitant increases in hedge management costs, many hedges have been neglected and gradually replaced by more convenient post-and-wire fencing (JONES *et al.* 2001). Furthermore, the considerable damage caused by the bacterium *Erwinia amylovora* to fruit- and ornamental plant cultivation, led to statutory regulations to avoid the spread of the disease by grubbing the affected hawthorns and by cutting the infected parts (NATUURRESERVATEN 1996). In this way, many old hedges have disappeared in the course of the sixties and seventies. Nowadays *C. monogyna* is often replanted in landscape architectural projects. Based on the recent inventories, *C. laevigata* is less common in Flanders. It is characteristic for old hedges and wood banks on richer soil types. Although *C. ×media* is a hybrid, it appears to have a higher abundance than its parental species *C. laevigata*. According to MAES & RÖVEKAMP (1999) this may be due to the better adaptation ability of *C. ×media* to changing environments. To date, *C. rhipidophylla* has not been found in Flanders; in contrast to the putative hybrids of this taxon and *C. monogyna* on the one hand (*C. ×subsphaerica*, syn. *C. ×kyrtostyla*) and *C. laevigata* on the other hand (*C. ×macrocarpa*), which do occur in Flanders.

In this study we describe the morphological variation of leaves and fruits of the five indigenous *Crataegus* taxa in Flanders. Based on the inventories of autochthonous trees and shrubs (MAES & RÖVEKAMP 1998, MAES & RÖVEKAMP 1999, RÖVEKAMP *et al.* 2000, OPSTAELE 2001, MAES *et al.* 2003), individuals of the complex were sampled in different regions in Flanders. Starting from the classification described by CHRISTENSEN (1992), we investigated the usefulness and discriminating power of the assumed diagnostic morphological characters in the determination of *Crataegus* species in Flanders. A key question was whether the large number of taxonomic groups can be justified by means of morphological evidence. A clear delineation of the species and hybrids is basic and necessary information in order to organize the conservation of the taxa in a concrete way.

## MATERIAL AND METHODS

### DISTRIBUTION MAPS

Maps were produced with ARCVIEW GIS version 3.1 (ESRI, Inc.) using data from the inventories of autochthonous trees and shrubs performed under the authority of the Flemish Community (MAES & RÖVEKAMP 1998, MAES & RÖVEKAMP 1999, RÖVEKAMP *et al.* 2000, OPSTAELE 2001, MAES *et al.* 2003). Surveyed locations (with an average size of 1.5 ha; VAN DER MIJNSBRUGGE 2003) were designated on the distribution maps with co-ordinates of a central point. These points indicate that the taxon is present in a surveyed location, but does not specify its local abundance.

### SAMPLING OF PLANT MATERIAL

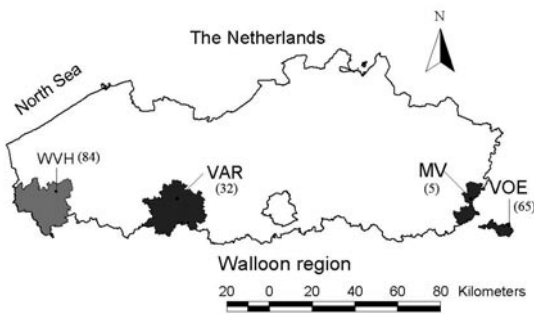
In total, 186 individuals of *Crataegus* were sampled in four regions of Flanders (Table 1, Fig. 1), based on the inventories of autochthonous trees and shrubs (MAES & RÖVEKAMP 1998, MAES & RÖVEKAMP 1999, RÖVEKAMP *et al.* 2000, OPSTAELE 2001, MAES *et al.* 2003). In these inventory databases, locations were chosen where the hawthorn populations of the studied complex had highest autochthonous score. For the attribution of these values of autochthony, several criteria were used that were derived from taxonomy, wood history and breeding history. These criteria are elaborated in MAES (1993) and MAES & BRINKKEMPER (2000: 26). All regions were sampled in autumn 2001, except for the region 'Voerstreek' which was sampled in autumn 2003. Large autochthonous populations were sampled purely at random (without a specific method), but for rare taxa, i.e. *C. ×macrocarpa* and *C. ×subsphaerica*, all individuals were sampled. Two reference samples of *C. ×subsphaerica* from Rhenen (the Netherlands) were included. Shrubs were identified in the field according to CHRISTENSEN (1992).

All sampled shrubs were marked with a plastic or wooden label that was attached with steel wire to the stem or to a thick branch.

Twigs with leaf material and/or fruits were collected from short shoots at man height and, if possible or applicable, at the side of the plant that was most exposed to sunlight. The sampled fruit and/or leaf twigs were labelled with the same code as used for the plants in the field. Furthermore, in the inventories mentioned above, all populations were indicated on a topographic map (1:25 000) and additional data (on habitat, soil, location and other vegetation, etc.) were included in the inventory forms (MAES & RÖVEKAMP 1998, MAES &

**Table 1.** Number of studied individuals (field identification according to CHRISTENSEN 1992) for each of the sampled areas in Flanders. MV: Maasvallei; VAR: Vlaamse Ardennen; VOE: Voerstreek; WVH: West-Vlaams Heuveland.

	MV	VAR	VOE	WVH	Total
<i>C. laevigata</i>	0	0	0	24	24
<i>C. monogyna</i>	2	22	45	30	99
<i>C. xmacrocarpa</i>	2	0	0	1	3
<i>C. xmedia</i>	0	8	20	24	52
<i>C. xsubsphaerica</i>	1	2	0	5	8
TOTAL	5	32	65	84	186



**Fig. 1.** The geographic distribution of the sampling sites in Flanders. The numbers indicate the number of sampled shrubs. The reference samples are not shown.

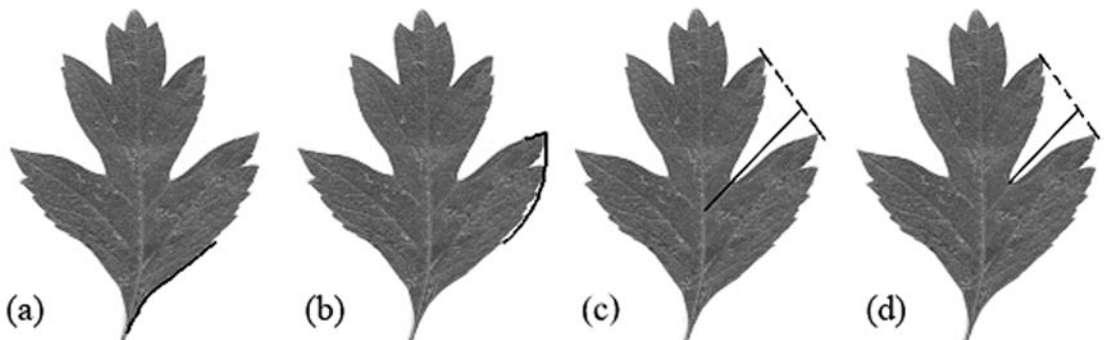
RÖVEKAMP 1999, RÖVEKAMP *et al.* 2000, OPSTAELE 2001, MAES *et al.* 2003).

Leaves were dried and fruits were conserved in 94% ethanol. The inventory data and the plant material are available from the Research Institute for Nature and Forest (Geraardsbergen, Belgium).

#### MORPHOMETRIC ANALYSIS

Of each sampled flowering shoot, three representative mature leaves were selected at random (without following any particular method). Different clusters of fruits were randomly collected from one twig and from this bulk, three fruits (omitting atypically or particularly large or small ones) were also randomly taken for further analysis.

Dried leaves were scanned at 200 dpi and measured with the digital imaging software IMAGE J version 1.32 (<http://rsb.info.nih.gov/ij/> Scion Corporation) (accuracy: 1 pixel, i.e., 0.125 mm). Height and width of the fruits (conserved in 94% ethanol) were measured with a sliding caliper (accuracy: 0.05 mm). The fruits were studied with a binocular stereoscope (WILD, M5) and measurements of sepals were performed using an eyepiece graticule (accuracy: 0.01 mm). The studied characters were based on CHRISTENSEN (1992), with field-determination table from MAES (after TIMMERMAN & MÜLLER 1994, CHRISTENSEN 1992). Because of the explorative nature of this study we focused on the characters that are applicable for field determination (Table 2, Fig. 2).



**Fig. 2.** Leaf measurements carried out in this study: (a) LWT; (b) LT; (c) LMI+DI; (d) DI.

**Table 2.** List of the studied morphological characters with abbreviations used and explanation of the possible states for SpSh and SpSt.

Structure	Character	Abbr.
<b>Leaf</b>		
	number of teeth on basal lobe	#T
	length of basal lobe without teeth	LWT
	length of basal lobe with teeth	LT
	length of basal lobe with teeth/length of basal lobe without teeth	LTWT
	depth of indentation	DI
	length of lamina from midrib to indentation	LMI
	depth of indentation/length of lamina from midrib to indentation	DILMI
<b>Fruit</b>		
	number of styles	#S
	height	FH
	width	FW
	height/width	FHW
<b>Sepals</b>		
	shape	SpSh
	standing	SpSt
	length	SpL
	width	SpW
	length/width	SpLW
<b>SpSh state</b>		
triangular	Sepals with straight sides	
concave	Sepals with concave sides.	
convex	Sepals with convex sides. In this case, the sepals are mostly shorter and less acute.	
variable	Sepals vary from sepals with straight or concave sides to sepals with convex sides, or sepals with two different types of sides.	
<b>SpSt state</b>		
spreading	The sepals are orientated more or less perpendicular to the vertical axis of the fruit	
sub-erect	The sepals are at an angle of more or less 45° with the upper plane of the fruit	
erect	The sepals stand more or less vertical on the upper plane of the fruit	
variable	The sepals have several orientations on 1 fruit or on different fruits of the same individual.	

## STATISTICAL ANALYSIS

Mean values were calculated for each individual. Exploratory data analyses were carried out by means of dot plots, box plots and cumulative distributions (S-PLUS 2000, MATHSOFT 1999) for the average values of the measurements and through frequency histograms (SPSS 11.0, SPSS 2001) for discrete characters to estimate the discriminating power of each morphological character. A character was determined as diagnostic for taxonomic identification if the box plots of different taxa did not overlap or if the frequency of the character was clearly higher (quantified by means of

the cumulative distributions) in one taxon. Based on exploratory data analyses, a few individuals were reclassified.

Principal Component Analysis (PCA) with the reclassified individuals was run several times to identify those characters which gave the best discrimination between taxa. The final PCA was performed based on five diagnostic morphological characters in S-PLUS 2000 (MATHSOFT 1999) using the mean values in order to visualise and investigate the possible relationships between five diagnostic characteristics. The five characters used for PCA were selected in such a way that they were mutually independent.

## RESULTS

DISTRIBUTION OF *CRATAEGUS* SPECIES IN FLANDERS

All taxa showed the highest concentration in the south of Flanders (Fig. 3), which is characterised by richer soil types. *C. monogyna* (31.9% of sampling sites, Fig. 3) was more common than *C. ×media* (18.6% of sampling sites, Fig. 3) which was in turn more abundant than *C. laevigata* (12.5% of sampling sites, Fig. 3). *C. ×macrocarpa* was more rare (1.8% of sampling sites, Fig. 3) than *C. ×subsphaerica* (3.8% of sampling sites, Fig. 3).

## COMPARISON BETWEEN THE FIVE TAXA IN FLANDERS

*C. monogyna* and *C. laevigata*

Our samples can be distinguished on the basis of morphological characters in two main groups that are not clearly separated (Fig. 4). For a number of characters the distinction between the *C. monogyna* group and the *C. laevigata* group is obvious. The leaves of *C. monogyna* have in general deeper indentations (Fig. 5) and the sepals from the fruit of *C. monogyna* are longer and narrower. In addition, the leaves of *C. monogyna* have fewer teeth at the basal lobe.

The majority of *C. monogyna* individuals have one style, whereas *C. laevigata* has two or rarely three styles (Fig. 6). Sepal width (SpW) also appears important for distinguishing both species. Fruits of *C. laevigata* are in general broader and smaller and the sepals are in general shorter than the ones of *C. monogyna*, although some overlap exists (Table 5).

*Intermediate forms*

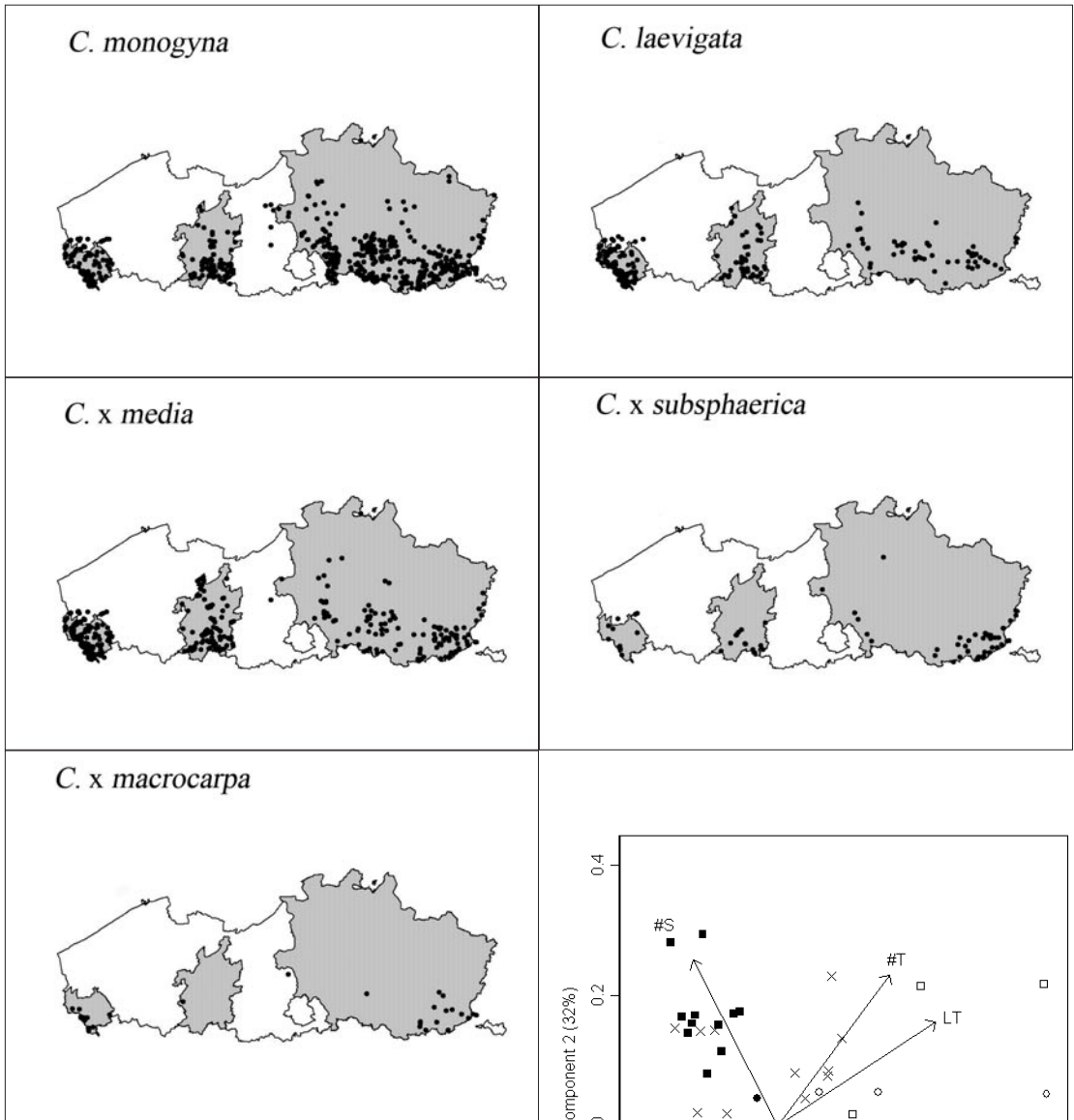
Individuals of the putative hybrid *C. ×media* are remarkably distributed between and throughout the clusters of the parental taxa because most of the characters studied show great overlap. The PCA biplot does not reveal a discrete and intermediate position between the *C. monogyna*-group and the *C. laevigata*-group. For some characters we measured a large range that exceeded the ranges of one or both parental species.

*C. ×subsphaerica* is more or less distinct from *C. monogyna* on the basis of the serration of the leaves and the number of teeth at the basal leaf lobe. *C. ×subsphaerica* has in general more teeth on the basal lobe than *C. monogyna*, but a great overlap of the ranges was observed. Fig. 7a indicates that Sepal length (SpL) is the most distinguishing fruit character because mean values for this character are quite different and *C. ×subsphaerica* can have much longer sepals than *C. monogyna*. However, large overlap exists for SpL. When outliers are not taken into account, *C. ×subsphaerica* seems to have in general slightly bigger fruits than *C. monogyna*.

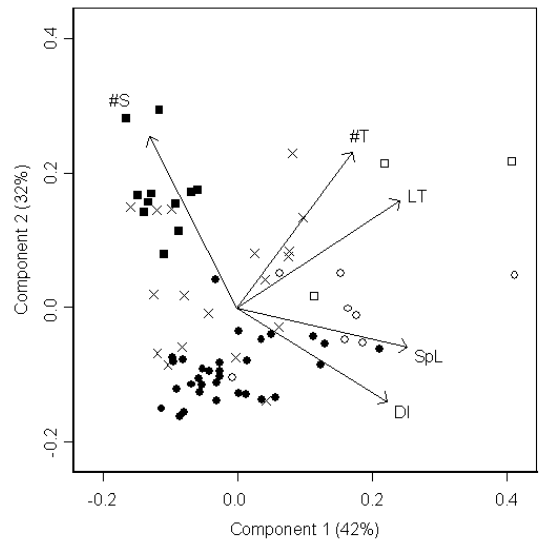
The three individuals of *C. ×macrocarpa* deviate remarkably from the other taxa in a number of characters, in particular in the serration of the basal lobe (LTWT and #T) and in fruit height (FH) (Table 5, Fig. 7). Sepal standing (SpSt) also appears to make distinction between *C. ×macrocarpa* and the other taxa studied (in particular to *C. laevigata*), but this character is less important.

**Table 3.** All five component values of the principal component analysis based on diagnostic morphological characters. The numbers represent eigenvectors.

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5
Sepal length	0.541	0.141	0.563	0.609	0.000
Length of basal lobe with teeth	0.516	0.391	0.354	0.000	0.673
Depth of indentation	0.478	0.338	0.634	0.000	0.496
Number of styles	0.278	0.624	0.263	0.638	0.240
Number of teeth on basal lobe	0.369	0.568	0.294	0.460	0.493



**Fig. 3.** Distribution of the 5 indigenous *Crataegus* taxa in Flanders based on data of inventories of autochthonous trees and shrubs in Flanders (MAES & RÖVEKAMP 1998, MAES & RÖVEKAMP 1999, RÖVEKAMP *et al.* 2000, OPSTAELE 2001, MAES *et al.* 2003). Surveyed areas are in grey; areas that were not yet sampled and surveyed are in white.



**Fig. 4.** Biplot of the first two principal components performed with the reclassified individuals.  
 ●: *C. monogyna*, ×: *C. x media*, ■: *C. laevigata*, ○: *C. x subsphaerica*, □: *C. x macrocarpa*

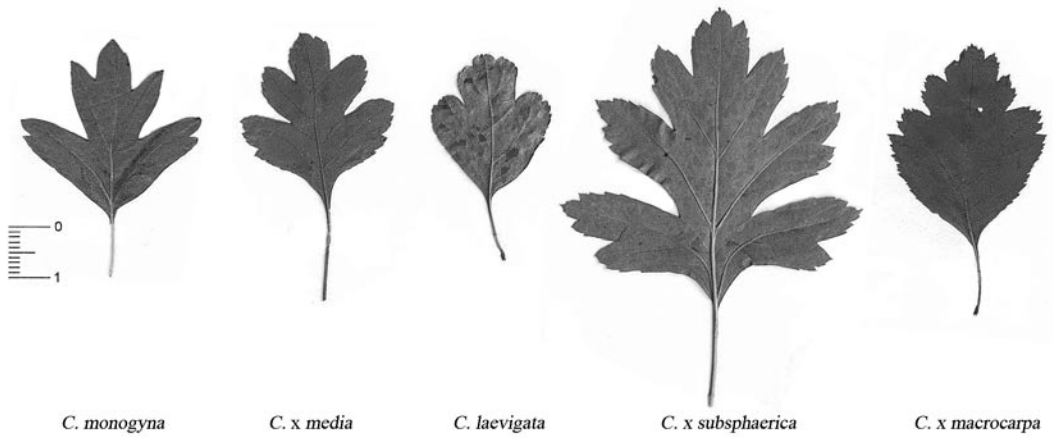


Fig. 5. Contrasting leaf morphologies between different *Crataegus* taxa in Flanders.

Table 4. Importance of components (standard deviation and proportion of total variance accounted for by each axis).

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5
Standard deviation	1.455	1.270	0.822	0.603	0.480
Proportion of variance	0.423	0.323	0.135	0.073	0.046
Cumulative proportion	0.423	0.746	0.881	0.954	1.000

DISCUSSION

DISTRIBUTION OF *CRATAEGUS* SPECIES IN FLANDERS

The distribution of *C. x media* and its parental taxa (*C. monogyna* and *C. laevigata*) in Flanders is more or less restricted to the south. Although *C. x media* is a hybrid, the maps (Fig. 3) indicate (locally) a higher abundance than its parental species. As a pioneer species, *C. monogyna* is more abundant than *C. laevigata*. The latter has more strict ecological requirements. *C. x media*, the natural hybrid, has an intermediate abundance. This may point to a better adaptability of *C. x media* compared to *C. laevigata* (THOMAS & VANDER MIJNSBRUGGE 2001). This phenomenon has been observed for other species, e.g.

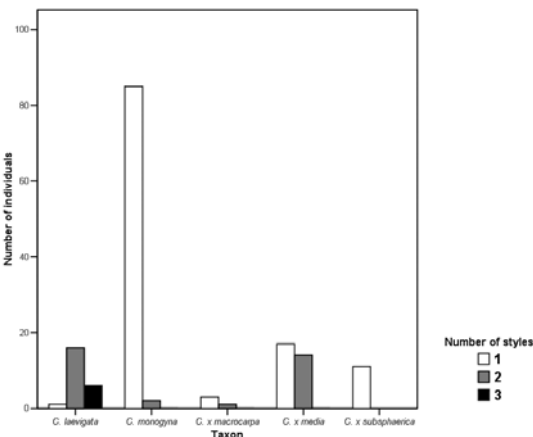


Fig. 6. Histogram of the number of styles for each taxon.



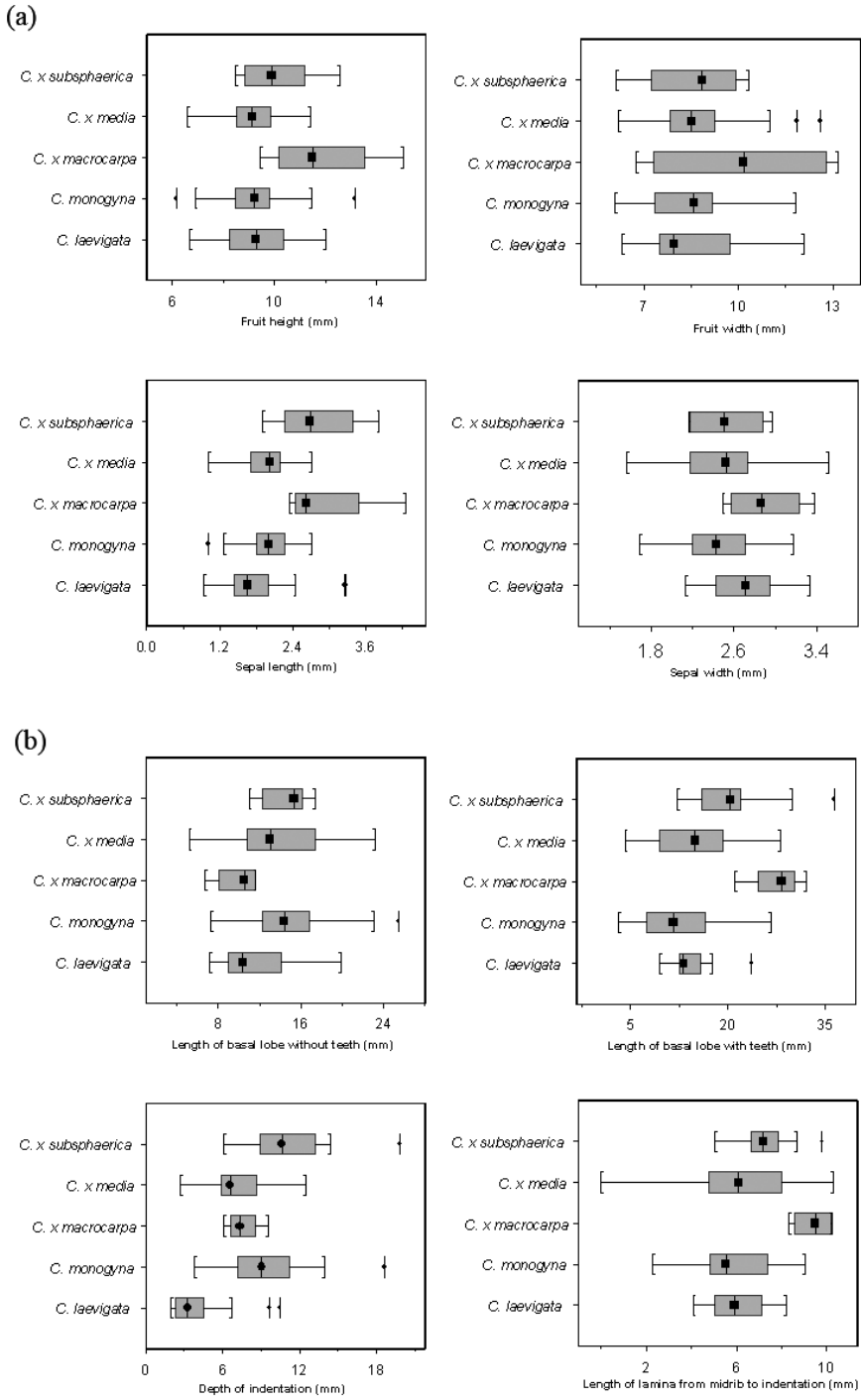


Fig. 7. Boxplots of major fruit (a) and leaf (b) characters. ■: mean value, ●: outlier.

indigenous *Prunus ×fruticans* in Flanders, which shows a higher abundance than its putative parental species *P. domestica* subsp. *insititia* (K. VANDER MIJNSBRUGGE, pers. obs.).

#### COMPARISON BETWEEN THE FIVE TAXA IN FLANDERS

##### *C. monogyna* and *C. laevigata*

This study confirms that the great majority of individuals of *C. monogyna* have 1 style, whereas *C. laevigata* has 2 or rarely 3 styles. However, according to CHRISTENSEN (1992) the occurrence of 2 styles is not unusual for *C. monogyna*. In this study, two individuals classified as *C. monogyna* in the field, had two styles. But analysis of the leaf characters (depth of indentation, serration) in these individuals suggests that they probably belong to *C. ×media*. Most likely, these individuals have a number of persistent characters from the *C. monogyna* parent. Because of several generations of backcrossing with *C. ×media* other typical characters of *C. monogyna* have shifted in various degrees towards *C. ×media*.

Similarly, the observed individuals of *C. laevigata* bearing fruits with one style are most likely individuals of *C. ×media* as well. Further analysis revealed that the indentation of the leaves is rather deep and the number of teeth rather high for typical individuals of *C. laevigata*. In general, *C. laevigata* has more superficial leaf indentations and more teeth on the basal lobe than *C. monogyna*. Two individuals had more than 15 teeth. These individuals most likely belong to *C. ×media* and, as the result of backcrossing, showed characters (i.e. serration of the leaves) of *C. monogyna*. One individual classified as *C. laevigata* showed extremely low serration of the basal leaf lobe and two individuals showed extremely high serration of the basal leaf lobe. These individuals appeared to be misidentified, and it was concluded that the individual with 3 teeth on the basal leaf lobe belongs to *C. monogyna* and that the two individuals with 18 teeth are most likely *C. ×media*. This is remarkable because, in general, *C. ×media* has more teeth than *C. monogyna* and fewer than *C. laevigata*.

##### *Intermediate forms*

The presence of intermediate forms indicates a process of successive natural backcrossings that blur the species boundaries. Based on morphological characters, the putative hybrid *C. ×media* forms a continuous hybrid swarm between the two parental species (*C. laevigata* and *C. monogyna*). This taxon has for a couple of characters a larger range than the parental taxa. The most reliable character for identification of *C. ×media* is the number of styles. It is the only taxon on which one individual often bears fruits with either one or two styles. In general, *C. ×media* has more teeth than *C. monogyna* and the indentation is usually more superficial. However, these characters are ambiguous because *C. ×media* shows large overlap with *C. monogyna*.

GOSLER *et al.* (1994) stated that *C. monogyna* has a large phenotypic plasticity in leaf shape and leaf size. In contrast to the large phenotypic plasticity of the leaves of different *C. monogyna* individuals, analysed fruit characteristics appear to be less variable. For all taxa studied our results reveal on average lower values for the proportion of the fruit height to the fruit width and for the proportion of the sepal length to the sepal width than those reported by CHRISTENSEN (1992). These findings suggest that fruits of hawthorn in Flanders are less elongated and have broader triangular sepals. One hypothesis is that the populations of the *Crataegus* taxa in Flanders are genetically distinct from other populations in Europe, which might be manifested in congruent phenotypic differences. Another explanation may be the occurrence of hybridisation and backcrossing with one of the parents by which particular characters become more (or less) explicit. Furthermore, fruit size and shape can be partly influenced by climate and/or soil parameters. The broader triangular shape of the sepals is possibly related to the rounded shape of the fruits: the more the fruits are rounded, the wider the upper surface of the fruits and the more free space for implantation of the sepals.

*C. ×subsphaerica* is morphologically difficult to distinguish from *C. monogyna*. Only the

**Table 5.** Compared characteristics of *C. monogyna*, *C. laevigata*, *C. xmedia*, *C. xsubspaeirica* and *C. xmacrocarpa*. Bold characters indicate the main discriminant characters. Numbers between brackets indicate outliers, numbers between square brackets the mean values. The columns 'Literature' refer to the results published by CHRISTENSEN (1992). The leaf characters LTWT, DILMI and #T are not comparable with the data in CHRISTENSEN (1992).

character	<i>C. monogyna</i>		<i>C. laevigata</i>		<i>C. xmedia</i>		<i>C. xsubspaeirica</i>		<i>C. xmacrocarpa</i>	
	literature	our results	literature	our results	literature	our results	literature	our results	literature	our results
Length of basal lobe with teeth/ Length of basal lobe without teeth		<b>0.2-3.5 [0.8]</b>		<b>0.6-2.3 [1.4]</b>		<b>0.2-3.2 [1.5]</b>		<b>0.6-2.4 [1.3]</b>		<b>1.8-4.8 [2.5]</b>
<b>Depth of indentation/ Length of lamina from midrib to indentation</b>		<b>0.6-7.0 [1.5]</b>		<b>0.3-1.0 [0.6]</b>		<b>0.6-1.9 [0.9]</b>		<b>0.7-2.7 [1.8]</b>		<b>0.7-1.4 [0.8]</b>
<b>Number of teeth on basal lobe</b>		<b>mostly 1-10, sometimes 11-15</b>		<b>mostly 6-15</b>		<b>1-15 (-20)</b>		<b>mostly 3-20, sometimes more</b>		<b>6-30</b>
Number of styles	1 (-2)	mostly 1	(1-) 2-3 (-5)	mostly 2, sometimes 3	1-2 (-3)	1 or 2	1 (-2)	1 (-2)	1-2 (-3)	1 or 2
Fruit height (mm)	6-11	(6.2-) 6.9-11.5 (-13.1) [9.2]	6-14	6.7-10.5 [8.9]	5-11	(6.6) 8.3-11.4 [9.5]	7-14	7.2-12.6 [9.2]	6-13	9.4-12.0 (15.0) [11.3]
Fruit width (mm)	5-10	6.1-11.4 [8.7]	6-12	6.3-9.7 (-11.8) [7.8]	5-10	6.2-12.6 [8.9]	5-12	6.1-10.3 [8.2]	5-13	(6.8) 7.9-13.2 [11.1]
Fruit height/Fruit width	1.0-2.0	0.9-1.3 (-1.5) [1.1]	1.0-1.4 (-1.8)	(0.9-) 1.0-1.3 [1.1]	1.0-1.3 (1.6)	0.9-1.3 [1.1]	1.1-1.8	(0.9-) 1.0-1.3 (-1.4) [1.1]	1.0-1.8	0.86-1.40
Sepal standing	reflexed, rarely erect to spreading	mostly spreading, less frequently reflexed or sub-erect	recurved or spreading	mostly sub-erect, but also often erect or spreading	reflexed	spreading or sub-erect, sometimes erect	reflexed or spreading (var. <i>kyrtosrpha</i> ), erect or erect to spreading (var. <i>domicensis</i> )	mostly spreading or sub-erect, sometimes reflexed or erect	reflexed or spreading (var. <i>macrocarpa</i> ), erect-suberect ( <i>hadensis</i> )	erect, reflexed, sub-erect, sometimes spreading
<b>Sepal length (mm)</b>	<b>1.2-4.4</b>	<b>1.3-2.7 [2.0]</b>	<b>0.9-2.8</b>	<b>0.9-2.2 [1.5]</b>	<b>1.9-3.3</b>	<b>1.3-2.7 [2.0]</b>	<b>1.9-5.1</b>	<b>2.2-3.8 [2.6]</b>	<b>1.8-4.9</b>	<b>1.8-3.3 (4.3) [2.5]</b>
Sepal width (mm)	1.2-2.6	1.7-3.2 [2.4]	1.4-2.6	2.2-3.3 [2.7]	1.8-3.5	(1.6) 1.8-3.1 (-3.5) [2.7]	1.8-3.0	1.7-3.0 [2.3]	1.6-3.7	2.5-3.4 [2.7]
<b>Sepal length / Sepal width</b>	<b>0.7-1.8</b>	<b>0.6-1.4 [0.8]</b>	<b>0.7-1.3 (-1.5)</b>	<b>0.3-0.9 (-1.6) [0.6]</b>	<b>0.6-1.1 (-1.9)</b>	<b>(0.5-) 0.7-1.2 [0.8]</b>	<b>0.9-2.2</b>	<b>0.8-1.4 [1.1]</b>	<b>1.0-2.2</b>	<b>0.7-1.3 [0.91]</b>

length of the sepals and the length of the serrate part of the basal lobe differ from *C. monogyna*. This can be due to the smaller sampling size or because the identification in the field was based (only) on these characters. The individuals described as *C. xsubsphaerica* can be considered as individuals of *C. monogyna* with exceptional long sepals and/or with strongly serrate leaves. But on the other hand, if the original (and typical) hybrid has backcrossed over several generations with *C. monogyna*, all characters but those two can have completely faded (and become indistinct) within the frame of the phenotypic variation of the *C. monogyna* parent.

The putative hybrid between *C. laevigata* and *C. rhipidophylla*, *C. xmacrocarpa*, can be distinguished by the higher and broader fruits and the very long sepals. The leaves of *C. xmacrocarpa* have more teeth on the basal lobe and deeper indentations than those of *C. laevigata*. The difference between the individual of *C. xmacrocarpa* from West-Vlaams Heuvelland and individuals of *C. laevigata* is less obvious.

It seems that the putative *C. xmacrocarpa* population of West-Vlaams Heuvelland (Fig. 3e) is the result of several generations of backcrossings with *C. laevigata* (or *C. xmedia*), resulting in increased parental characters at the expense of the characters of the original hybrids. The population from Riemst is presumably the only typical population of *C. xmacrocarpa* in Flanders. Although only two individuals were analysed in detail, more shrubs with similar phenotypes were noticed during field visits.

### *C. rhipidophylla*

The extinction of *C. rhipidophylla* in Flanders remains an intriguing question. Although the occurrence of *C. xsubsphaerica* in Flanders is uncertain, the more obvious population of *C. xmacrocarpa* in Riemst points to a historical presence of *C. rhipidophylla* in Flanders. *C. rhipidophylla* is considered a boreal species (CHRISTENSEN 1992). It can be assumed that the species migrated through Flanders after the last glaciation and only the hybrids survived through inheritance of competitive power from the parental taxa. *C. rhipidophylla* has also

been observed in Denmark (CHRISTENSEN 1996) and in Central Europe (Romania; B. MAES, pers. comm.). On the other hand, it can be hypothesised that *C. rhipidophylla* never occurred in Flanders and that only the hybrids migrated as far as Flanders after the last glacial age. In this case *C. rhipidophylla* itself migrated out of the southern refugia through Central Europe towards the north.

Characters suggested by CHRISTENSEN (1992) for discrimination between *C. laevigata* and *C. monogyna* are useful, but distinction between hybrid taxa appears more difficult on the basis of the characters mentioned in the literature. As we did not identify characters that unambiguously discriminate hybrids, a combination of different intermediate characters (e.g. serration of the leaves, indentation and sepal length) has to be used to classify a shrub as *C. xmedia*, *C. xsubsphaerica* or *C. xmacrocarpa*. Especially the combination of the number of styles, the serration and the indentation of leaves appear to be useful to distinguish the taxa that occur in Flanders.

From this point of view, distinction between varieties based on one character (as within *C. xsubsphaerica* and *C. xmacrocarpa*) as suggested by CHRISTENSEN (1992) is ambiguous, as a lot of characters seem to overlap between species and even their hybrid taxa. Most likely the populations studied by CHRISTENSEN (1992) have more pronounced characters than the populations occurring in Flanders. Strong hybridisation and backcrossing in Flanders may have resulted in blurring of distinguishing characters and have led to continuous hybrid swarms.

Therefore, further research is needed; in particular molecular genetic analyses have been shown to add useful complementary information in hybridisation studies about genetic differentiation, heterozygosity and diversity within and between populations. A molecular marker analysis on *Crataegus* in Flanders is carried out at the CLO-Department for Plant Genetics and Breeding (Melle, Belgium).

Finally, in this explorative study only a relatively small number of leaves and fruits per sampled shrub were included. Therefore, results should be interpreted with caution. For the construction of a representative taxonomic key for Flanders more

repetitions of these highly variable taxa should be considered.

### ACKNOWLEDGEMENTS

We are grateful to Pierre Hubeau for skilful field assistance and Peter Chaerle for technical support of Image J and scanning of leaf material. This research was partially funded by a PhD grant of the Institute for the Promotion of Innovation through Science and Technology in Flanders (IWT-Vlaanderen).

### REFERENCES

- ARNOLD M.L., 1997. — *Natural hybridisation and evolution*. Oxford Series in Ecology and Evolution. Oxford University Press, New York – Oxford.
- BYATT J.I., 1975. — Hybridisation between *Crataegus monogyna* Jacq. and *C. laevigata* (Poiret) DC in south-eastern England. *Watsonia* **10**: 253-264.
- CHRISTENSEN K.I., 1992. — Revision of *Crataegus* sect. *Crataegus* and nothosec. Crataeguineae (Rosaceae-Maloideae) in the Old World. *Systematic Botany Monographs* **35**: 199 p.
- CHRISTENSEN K.I., 1996. — A reanalysis of the status of *Crataegus eremitagensis*, *C. raavadensis* and *C. schumacheri*. *Acta Univ. Ups. Symb. Bot. Ups.* **31**: 211-220.
- CROXTON P.J. & SPARKS T.H., 2002. — A farm-scale evaluation of the influence of hedgerow cutting frequency on hawthorn (*Crataegus monogyna*) berry yields. *Agric., Ecosyst. Environm.* **93**: 437-439.
- DICKINSON T.A. & CAMPBELL C.S., 1991. — Population structure and reproductive ecology in the Maloideae (Rosaceae). *Syst. Bot.* **16**: 350-362.
- GOSLER A.G., KELLY C.K. & BLAKEY J.K., 1994. — Phenotypic plasticity in leaf morphology of *Crataegus monogyna* (Rosaceae): an experimental study with taxonomic implications. *Bot. J. Linn. Soc.* **115**: 211-219.
- JONES A.T., HAYES M.J. & SACKVILLE HAMILTON N.R., 2001. — The effect of provenance on the performance of *Crataegus monogyna* in hedges. *J. Appl. Ecol.* **38**: 952-962.
- KENNEDY C.E.J. & SOUTHWOOD T.R.E., 1984. — The number of species of insects associated with British trees: a re-analysis. *J. Anim. Ecol.* **53**: 455-478.
- MACDONALD D.W. & JOHNSTON P.J., 1995. — The relationship between bird distribution and the botanical and structural characteristics of hedges. *J. Appl. Ecol.* **32**: 492-505.
- MAES N., 1993. — *Genetische kwaliteit van inheemse bomen en struiken. Deelproject: Randvoorwaarden en knelpunten bij behoud en toepassing van inheems genemateriaal*. IBN-rapport 20, IKC-NBLF, IBN-DLO, Wageningen, The Netherlands.
- MAES N. & RÖVEKAMP C., 1998. — *Oorspronkelijk inheemse bomen en struiken in Vlaanderen. Een onderzoek naar autochtone genenbronnen in de Ecologische Impulsgebieden*. Ministerie van de Vlaamse Gemeenschap, Afdeling Bos & Groen, Brussel, Belgium.
- MAES B. & RÖVEKAMP C., 1999. — *Cursus autochtone bomen en struiken Vlaanderen (een productie van het Ekologisch Adviesburo Maes en BRONNEN)*. Educatief bosbouwcentrum Groenendaal, Brussel, Belgium.
- MAES B. & BRINKKEMPER O., 2000. — *Autochtone bomen en struiken, een historisch-ecologische benadering*. Jaarboek voor Ecologische Geschiedenis, Gent-Thorn 2000, pp. 15-35.
- MAES N., RÖVEKAMP C., OPSTAELE B. & ZWAENEPOEL A., 2003. — *Oorspronkelijke inheemse bomen en struiken in de houtvesterijen Antwerpen en Turnhout*. Ministerie van de Vlaamse Gemeenschap, afdeling Bos en Groen, Brussel, Belgium.
- MATHSOFT, 1999. — *S-PLUS 2000 Professional*. MathSoft Inc., Seattle, Washington, USA.
- OPSTAELE B., 2001. — *Autochtone bomen en struiken in de houtvesterijen Leuven en Hasselt*. Ministerie van de Vlaamse Gemeenschap, afdeling Bos & Groen, Brussel, Belgium.
- OSBORNE P., 1984. — Bird numbers and habitat characteristics in farmland hedgerows. *J. Appl. Ecol.* **21**: 63-82.
- PHIPPS J.B. & MUNIYAMA M., 1980. — Studies in *Crataegus* L. (Rosaceae: Maloideae). III. A taxonomic revision of *Crataegus* (Rosaceae) in Ontario. *Can. J. Bot.* **58**: 1621-1699.
- PHIPPS J.B., O'KENNON R.J. & LANCE R.W., 2003. — *Hawthorns and medlars*: 139 p. RHS Plant Collector Guide. Timber Press, Portland, OR.
- RÖVEKAMP C., MAES N. & ZWAENEPOEL A., 2000. — *Oorspronkelijk inheemse bomen en struiken en cultuurwilgen in de Vlaamse Vallei. Een onderzoek naar autochtone genenbronnen in Gent en omgeving*. Ministerie van de Vlaamse Gemeenschap, Afdeling Bos & Groen, Brussel, Belgium.
- SPARKS T.H., PARISH T. & HINSLEY S.A., 1996. — Breeding birds in field boundaries in an agri-

- cultural landscape. *Agric., Ecosyst. Environm.* **60**: 1-8.
- SPARKS T.H. & MARTIN T., 1999. — Yields of hawthorn *Crataegus monogyna* berries under different hedgerow management. *Agric., Ecosyst. Environm.* **72**: 107-110.
- SPSS INC., 2001. — *SPSS 11.0*. SPSS Inc., Chicago, USA.
- THOMAES A. & VANDER MIJNSBRUGGE K., 2001. — Rozen en meidoornen. Hoe autochtoon zijn onze bomen en struiken? *Groene Band - Tijdschrift van de Vereniging voor Bos in Vlaanderen* **113**: 21-33.
- TIMMERMAN G. & MÜLLER T., 1994. — *Wildrosen und Weißdorne Mitteleuropas Landschaftsgerechte Sträucher und Bäume*, 2. Aufl. Schwäbischen Albvereins, Stuttgart, Germany.
- VANDER MIJNSBRUGGE K., 2003. — Conservation of the heritage of autochthonous woody plants in Flanders (Belgium). *Scripta Botanica Belgica* **24**: 105-115.