



**Knowledge document for risk  
analysis of the non-native  
*Mimulus guttatus*  
in the Netherlands**

**by**

**K.R. Koopman, R. Beringen, F.P.L. Collas, J. Matthews,  
B. Odé, R. Pot, L.B. Sparrius, J.L.C.H. van Valkenburg,  
L.N.H. Verbrugge & R.S.E.W. Leuven**

# Knowledge document for risk analysis of the non-native Monkeyflower (*Mimulus guttatus*) in the Netherlands

K.R. Koopman, R. Beringen, F.P.L. Collas, J. Matthews, B. Odé, R. Pot,  
L.B. Sparrius, J.L.C.H. van Valkenburg, L.N.H. Verbrugge  
& R.S.E.W. Leuven

21 September 2012

Radboud University Nijmegen,  
Institute for Water and Wetland Research  
Department of Environmental Science,  
FLORON & Roelf Pot Research and Consultancy

Commissioned by  
Invasive Alien Species Team  
Office for Risk Assessment and Research  
Netherlands Food and Consumer Product Safety Authority  
Ministry of Economic Affairs, Agriculture and Innovation

# Series of Reports on Environmental Science

The series of reports on Environmental Science are edited and published by the Department of Environmental Science, Institute for Water and Wetland Research, Radboud University Nijmegen, Heyendaalseweg 135, 6525 AJ Nijmegen, The Netherlands (tel. secretariat: + 31 (0)24 365 32 81).

## Reports Environmental Science nr. 415

- Title: Knowledge document for risk analysis of the non-native Monkeyflower (*Mimulus guttatus*) in the Netherlands
- Authors: Koopman, K.R., R. Beringen, F.P.L. Collas, J. Matthews, B. Odé, R. Pot, L.B. Sparrius, J.L.C.H. van Valkenburg, L.N.H. Verbrugge & R.S.E.W. Leuven
- Cover photo: *Mimulus guttatus* with *Juncus effusus* (tussock of stiff leafless stems) and *Lotus uliginosus* (smaller leaves and flowers) surrounded by *Crassula helmsii* in a clay excavation pit near Udenhout, The Netherlands (Photo: R. Beringen)
- Project manager: Dr. R.S.E.W. Leuven, Department of Environmental Science, Institute for Water and Wetland Research, Radboud University Nijmegen, Heyendaalseweg 135, 6525 AJ Nijmegen, the Netherlands, e-mail: [r.leuven@science.ru.nl](mailto:r.leuven@science.ru.nl)
- Project number: 62001590
- Client: Netherlands Food and Consumer Product Safety Authority, Office for Risk Assessment and Research, Invasive Alien Species Team, P.O. Box 43006, 3540 AA Utrecht
- Reference client: TRC/NVWA/2012/2009, order nr. 60400891, formdesk nr. 19460, specification code 6300004
- Orders: Secretariat of the Department of Environmental Science, Faculty of Science, Radboud University Nijmegen, Heyendaalseweg 135, 6525 AJ Nijmegen, the Netherlands, e-mail: [secres@science.ru.nl](mailto:secres@science.ru.nl), mentioning Reports Environmental Science nr. 415
- Key words: Dispersal; ecological effects; invasibility; invasiveness; non-indigenous species; weed control

Printed on environmentally friendly paper

© 2012. Department of Environmental Science, Faculty of Science, Institute for Water and Wetland Research, Radboud University Nijmegen, Heyendaalseweg 135, 6525 AJ Nijmegen, The Netherlands

*All rights reserved. No part of this report may be translated or reproduced in any form of print, photoprint, microfilm, or any other means without prior written permission of the publisher.*

# Contents

Summary .....	3
1. Introduction .....	5
1.1. Background and problem statement .....	5
1.2. Research goals.....	5
1.3. Outline and coherence of research .....	6
2. Materials and methods.....	8
2.1. Literature review .....	8
2.2. Data acquisition on current distribution .....	8
2.3. Additional field surveys .....	8
3. Species description .....	10
3.1. Nomenclature and taxonomical status .....	10
3.2. Species characteristics .....	11
3.3. Differences with visually similar species .....	13
3.4. Reproductive strategy.....	13
4. Habitat description .....	14
4.1. Habitat characteristics .....	14
4.2. Associations with other species .....	17
5. Distribution, dispersal and invasiveness.....	19
5.1. Global distribution.....	19
5.2. Current distribution in the Netherlands.....	20
5.3. Pathways and vectors for dispersal .....	25
5.4. Invasiveness.....	26
6. Impacts .....	27
6.1. Ecological effects.....	27
6.2. Socio-economical effects.....	29
6.3. Public health effects .....	29
7. Available risk classifications .....	30
7.1. Formal risk assessments .....	30
7.2. Other risk classifications .....	30
8. Management options.....	31
8.1. Prevention .....	31
8.2. Eradication and control measures.....	31

8.3. Ecosystem based management.....	32
9. Conclusions and recommendations .....	34
9.1. Conclusions.....	34
9.2. Effective management options.....	34
9.3. Recommendations for further research.....	34
Acknowledgements.....	35
References .....	36
Appendices .....	41
Appendix 1: Results of field surveys in 2012.....	41
Appendix 2: Accumulation capacities for different elements. ....	42
Appendix 3: Differences in accumulation between perennial and annual plants. ....	43

## Summary

The Monkeyflower (*Mimulus guttatus*) originated from the western part of North America. The native range of *M. guttatus* is spread throughout the western part of North America and ranges from Alaska to Northern Mexico. Outside of its native range, *M. guttatus* has invaded the eastern part of the United States and Canada, Western Europe, Russia, New Zealand and Tasmania. It was first recorded in the Netherlands in 1836 and over the past decade has displayed a rapid range extension. To support decision making with regard to the design of measures to prevent ecological, socio-economical public health effects, the Netherlands Food and Consumer Product Safety Authority (Ministry of Economic Affairs, Agriculture and Innovation) has asked to carry out a risk analysis of *M. guttatus* within the Dutch context.

A literature study was carried out to provide an overview of the current knowledge on the distribution and invasion biology of *M. guttatus* and to support a risk assessment within the Dutch context. Literature data were collected on the physiological tolerances, substrate preference, colonisation vectors, ecological and socio-economic impacts, public health effects and potential measures for management of this species. The literature study was largely internet based with use of university libraries. Various academic and non-academic search engines and websites were used in a systematic search of the Web of Knowledge, Scopus, Google Scholar and in an analysis of information available to the Dutch public, Google.nl. A summary of the results of the literature study is given in the following paragraphs.

Records of *M. guttatus* have been widely distributed throughout the Netherlands since 1950. The species occurs in small numbers along riverbanks, at sites that are flooded in winter. However, it seems that the larger populations are found in less dynamic, mesotrophic, moist habitats, where the vegetation is in an early succession stage. Population build-up can take place over several years, resulting in large populations of *M. guttatus* plants. Although field records are scarce, *M. guttatus* may be found in the semi-aquatic and terrestrial parts of the following habitat types of high conservation value: H2190 Humid dune slacks; H3130 Oligotrophic to mesotrophic standing waters with vegetation (*Littorelletea uniflorae*); H3260 Water courses of plain to mountainous levels (*Ranunculion fluitantis* and *Callitricho-Batrachion*); H3270 Rivers with muddy banks with *Chenopodium rubri* p.p. and *Bidention* p.p. vegetation.

The introduction of non-native aquatic macrophytes into a country has almost certainly been via the trade in live aquarium plants, legal or otherwise. *M. guttatus* is mainly used as an ornamental plant and therefore it is most likely that the species has been introduced to non-native habitats via horticulture and the ornamental plant trade. It is also introduced via wildflower seeds mixtures. Non-human mediated dispersal may occur via two mechanisms: seed setting and regeneration of fragmented parts. Seeds are buoyant and at an average daily flow velocity of  $0.28 \text{ m s}^{-1}$  seeds can be transported for 1 km downstream. However, some seeds retain buoyancy longer and at average daily flow velocities of  $0.82 \text{ m s}^{-1}$ , are able to disperse over a distance of 3 km. Dispersal through wind can only occur over short distances of several meters, whereas dispersal by animals like deer, birds and cattle can disperse seeds over 1 km

and possibly even further. Fragmentation can occur through rough hydrological conditions or herbivory. Fragments can have considerable regenerative capacities. Fragmentation may occur all year round and fragments may survive for up to 6 weeks which, in combination with high flow velocities, means that *M. guttatus* is able to disperse over very large distances throughout the year.

The impacts on native species in countries outside the Netherlands have been varied. The largest effect was observed in Scotland where negative effects on the species richness of the native riparian community induced local species replacement. However, most species that are impacted are widespread ruderal plants or other non-native species and thus possess no or only low conservation value. Furthermore, in other countries effects on species richness have been minimal. The relatively high light demand of *M. guttatus* hinders its competitive ability in habitats with strongly competitive plant species. In the Netherlands, *M. guttatus* is able to establish itself on disturbed riparian habitats but is eventually overgrown, through the course of vegetation succession, by taller perennial or woody plants like Reed (*Phragmites australis*) and Willows (*Salix* sp.).

*M. guttatus* is able to rapidly colonise disturbed sediment plots. After colonisation, the erect stem and rapid growth lead to physical habitat changes e.g. shading of surrounding plants and also changes to the structural diversity of vegetation. The results of a pot experiment show that *M. guttatus* has a higher soil nitrogen acquisition than the Henbit deadnettle (*Lamium amplexicaule*). This experiment indicates that the higher acquisition and subsequent reduction in nutrient availability by *M. guttatus* might reduce attractiveness of neighbouring species to pollinators in the field.

Knowledge on the prevention or removal of the *M. guttatus* is limited. Prevention should focus on the plant trade, since this is the main distribution channel. *M. guttatus* produces seeds that easily disperse via water and by animals. Therefore, dispersal out of introduced areas cannot be prevented. There is no evidence available to support a particular method of species-specific eradication or control measure. Cutting of the vegetation is a way to reduce reproduction. The best period for mowing seems to be before July because the ripening of seeds has already been observed in the Netherlands in early July. If the plants appear to be perennial or a hybrid then no management strategy is recommended and allowing vegetation succession to overgrow the plants seems the next best option to reduce the population size.

Formal risk assessments featuring *M. guttatus* have been carried out in Belgium and Ireland, both resulting in a low risk score.

# 1. Introduction

## 1.1. Background and problem statement

The Monkeyflower (*Mimulus guttatus*; Figure 1.1) originated from the western part of North-America and was first recorded in the Netherlands in 1836 (Mennema *et al.*, 1985). Over the past decade, this plant species showed a rapid range extension. At the start of this project, there was a lack of knowledge regarding the pathways for introduction, vectors for spread, key factors for establishment and invasiveness, and (potential) effects and management options of *M. guttatus* in the Netherlands.



**Figure 1.1:** Inflorescence of the Monkeyflower (*Mimulus guttatus*) on the banks of a clay excavation pit near Udenhout on July 12, 2012 (Photo: R. Beringen).

To support decision making with regard to the design of measures to prevent ecological, socio-economical and public health effects, the Netherlands Food and Consumer Product Safety Authority (Ministry of Economic Affairs, Agriculture and Innovation) has asked to carry out a risk analysis of *M. guttatus*. The present report reviews available knowledge and additional field data in order to underpin a risk assessment of the species.

## 1.2. Research goals

The major goals of this study are:

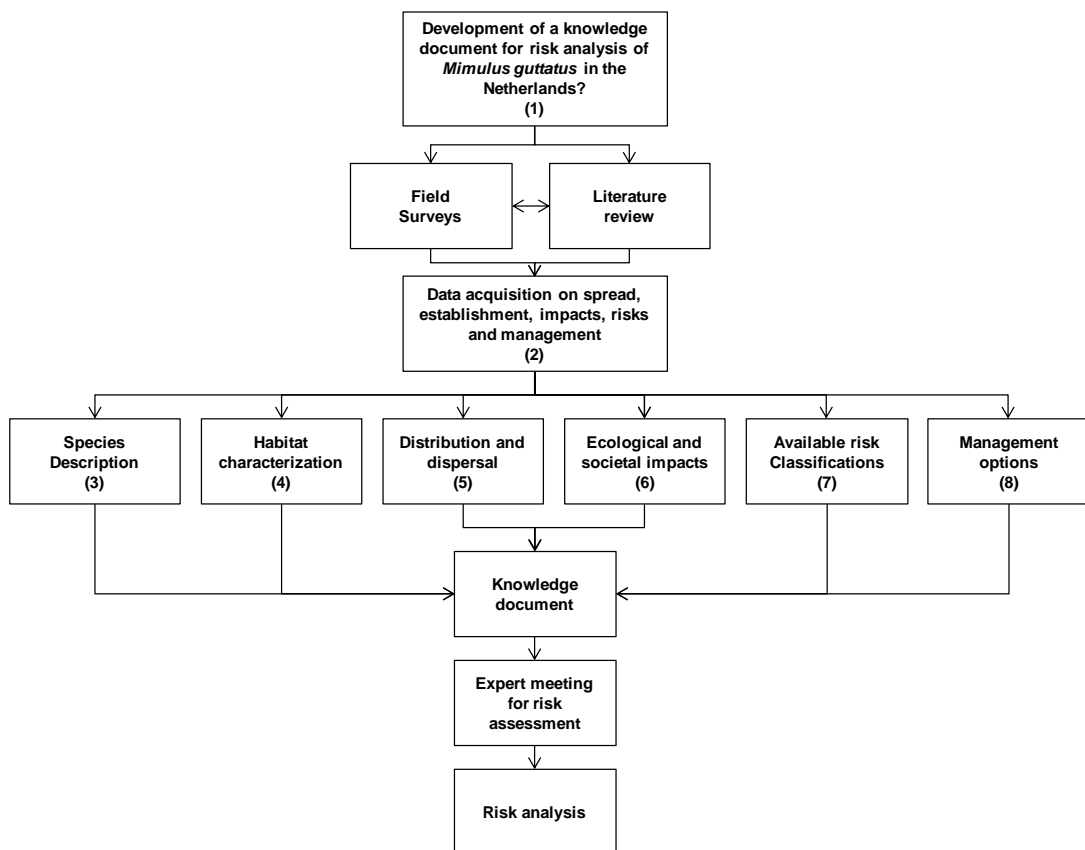
- To describe the species and habitat characteristics of *M. guttatus*.
- To describe the global distribution and to analyse the current spread of *M. guttatus* in the Netherlands.



- To identify the key factors for dispersal (pathways, vectors, invasiveness) and successful establishment of *M. guttatus*.
- To assess (potential) ecological, socio-economical and public health effects of *M. guttatus* in the Netherlands, taking into account the impacts of this species in other geographical areas.
- To summarize available risk classifications of *M. guttatus* in other countries.
- To review possible management options for control of spread, establishment and negative effects of *M. guttatus*.

### 1.3. Outline and coherence of research

The present chapter describes the problem statement, goals and research questions in order to identify key factors for the dispersal, establishment, effects and management of *M. guttatus* in the Netherlands. The coherence between various research activities and outcomes of the study are visualised in a flow chart (Figure 1.2).



**Figure 1.2:** Flow chart visualising the coherence of various research activities in order to develop a knowledge document for risk analysis of the Monkeyflower (*Mimulus guttatus*) in the Netherlands. The numbers in brackets refer to chapters of this report.

Chapter 2 gives the methodological framework of the project and describes the literature review, data acquisition and field surveys. Chapter 3 describes the identity, taxonomical status and reproductive biology of the species and briefly mentions

differences with visually similar species. The habitat characteristics and physiological tolerances of the species are summarized in chapter 4. The geographical distribution and trends in distribution in the Netherlands, including relevant pathways and vectors for dispersal are given in chapter 5. Chapter 6 analyses the ecological, economic and public health effects of the species. Results of formal risk assessments performed by other countries and available risk classifications of the species are summarized in chapter 7. Chapter 8 describes the scope of management options and focuses on prevention, eradication measures and control of the species. Finally, chapter 9 draws conclusions and gives recommendations for management and further research. Several appendices with raw data and background information complete this knowledge report. The report will be used as background information for an expert meeting in order to assess the dispersion, invasiveness, (potential) risks and management options of species in the Netherlands (Risk analysis).

## 2. Materials and methods

### 2.1. Literature review

A literature study was carried out to provide an overview of the current knowledge on the distribution and invasion biology of the Monkeyflower (*Mimulus guttatus*). Literature data were collected on the species traits, habitat characteristics, dispersal pathways, colonisation vectors, ecological, socio-economic and public health impacts, risk classifications and potential measures for management of this species. Our search was largely internet based with the additional use of university libraries. The literature research was conducted with the use of three different search engines: ISI Web of Knowledge, Scopus and Google Scholar. The first two engines were used with the search term *Mimulus guttatus*. In Google Scholar the following six search terms in combination with the Latin species name were used: control, dispersal, distribution, impact, management and vectors. The first fifty hits in Google Scholar were examined.

All articles found during the literature search were assessed on their relevance for this study and when relevant it was added to the database. The database consisted of the first author followed by the year and the title of the article. The search engine and search term used to find the specific article were also added. Following this, two keywords for the specific article were added to the database, which allowed specific searches of certain subjects. A short description of the content of each article was given, as well as the scientific status (peer reviewed, grey or anecdotic paper). The availability of each article was analyzed since not all articles were available in the libraries of Dutch universities or in the electronic public domain. Finally, the date of the search was indicated. The excel-file is available on request and contains all the articles acquired through the literature search.

A Google search (search terms: 'maskerbloem' and 'gele maskerbloem kopen') was performed to investigate whether *M. guttatus* is sold via the Dutch internet market.

### 2.2. Data acquisition on current distribution

Most data on geographical distribution of *M. guttatus* in the Netherlands originated from the National Database Flora & Fauna (NDFF). These data were complemented with data of herbarium specimens in the Q-bank Invasive Plants database (<http://www.q-bank.eu/Plants/>) and recent records in internet-based databases on nature sightings [www.waarneming.nl](http://www.waarneming.nl) and [www.telmee.nl](http://www.telmee.nl). Available data were stored in an excel file with year of record, x and y Amersfoort coordinates, number of kilometre square and data source. These data were subsequently used to map geographical distribution in several time periods and to analyse trends in species distribution.

### 2.3. Additional field surveys

Three sites with *M. guttatus* were visited on July 12 and 18, 2012: Westerpark in Amsterdam, a clay pit near Udenhout and a stream valley near Renkum (Appendix 1). These locations were selected from the distribution data for the following reasons:

- The population was present on the locations for several years;
- The population was relatively large;
- The species was growing in semi-natural or natural vegetation (e.g. not in intensively managed gardens).

Species, location, date of field search, coordinates, water depth (cm), transparency (Secchi depth in cm), pH, alkalinity ( $\text{meq l}^{-1}$ ), width of water body (m), water flow, water type, surface area covered by non-native species ( $\text{m}^2$ ), number of individuals/shoots and phenology were recorded (Appendix 1). The pH and alkalinity of the water were measured at the laboratory, using a ABU901 Autoburette in combination with TitraLabtm 80 (Radiometer, Copenhagen).

At each site, water and sediment samples were taken and these samples were stored in a refrigerator to allow future analysis of the physic-chemical properties.

At each site population size was estimated and the vegetation was described with a Tansley survey using the following abundance codes (DAFOR): d: dominant; a: abundant; f: frequent; o: occasional and r: rare. In addition, at each site plants were collected for herbarium specimens and DNA bar-coding.

### 3. Species description

#### 3.1. Nomenclature and taxonomical status

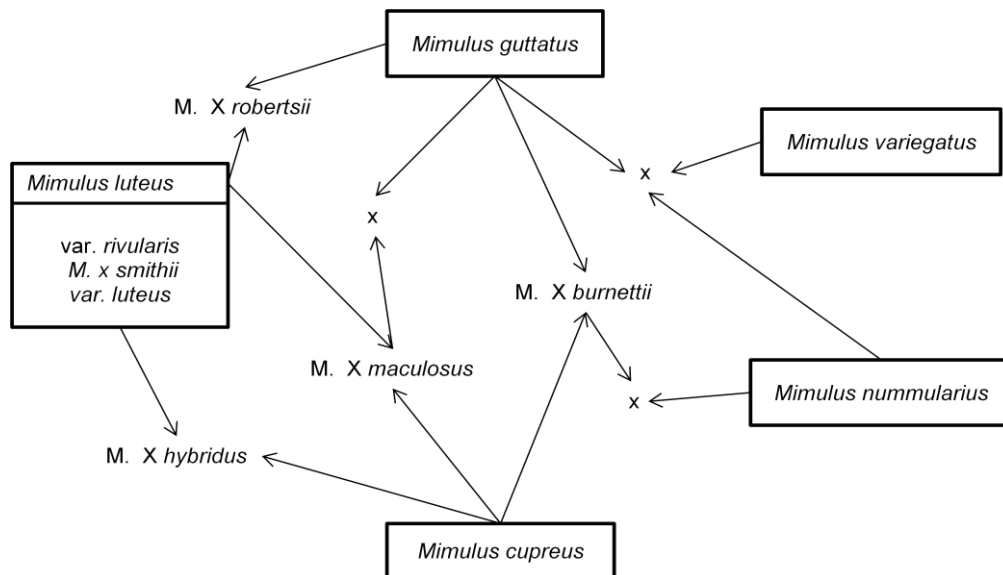
The Monkeyflower (*Mimulus guttatus*) is in fact a species complex. Several varieties and some different species are described within this complex (A.J. Silverdale; described in Rich & Jermy, 1998). Table 3.1 gives an overview of the nomenclature and taxonomical status of *M. guttatus*. The preferred English name is derived from Stace (1997). The addition 'common' is inappropriate because many plants outside the native biogeographical range of *M. guttatus* belong to the species complex. In the USA the prevailing name is Seep Monkey flower. The addition 'seep' seems practical for the native range, because in the USA various species can be distinguished. This species is able to hybridize with a number of other closely related species, referred to as *Mimulus* section *Simiolus*. An overview of species and possible hybrids in this plant section is given in figure 3.1.

**Table 3.1:** Nomenclature and taxonomical status of the Monkeyflower (*Mimulus guttatus*).

<p><b>Scientific name:</b>  <i>Mimulus guttatus</i> (Fischer, 1812) De Candolle, 1813</p>
<p><b>Synonyms:</b>  <i>Mimulus luteus</i> auct. non L.</p>
<p><b>Taxonomic tree</b><sup>1</sup>  Domain: Eukaryota  Kingdom: Plantae  Phylum: Tracheophyta  Class: Spermatopsida  Order: Lamiales  Family: Phrymaceae<sup>2</sup>  Genus: <i>Mimulus</i>  Species: <i>Mimulus guttatus</i></p>
<p><b>Preferred Dutch name:</b>  Gele maskerbloem</p>
<p><b>Other Dutch names:</b>  Not known</p>
<p><b>Preferred English name:</b>  Monkeyflower</p>
<p><b>Other English names:</b>  Common monkeyflower, Seep monkey flower</p>
<p><b>Native range:</b>  Western part of North America: ranges from Alaska to Northern Mexico; has an eastern boundary in Montana and South Dakota</p>
<p><b>Visually similar species:</b>  Several related species and hybrids within the species complex (<i>Mimulus moschatus</i> and some other Lamiales with large yellow flowers)</p>

1: According to Mabberley (2008), Naturalis Biodiversity Center (2012); 2: Mabberley (2008) uses Phrymaceae, Naturalis Biodiversity Center (2012) uses Phrygmaceae.

This report refers to *M. guttatus* as a species, but there are signs that some hybrids have been more commonly distributed in the United Kingdom than their parents, especially *M. x robertsii* (Lansdown, 2009). This might also be the case in the Netherlands. However, currently it is unknown whether hybrids occur in the Netherlands. This will require an extensive field survey. An identification key for hybrids in the *Mimulus* section *Simiolus* is developed by A.J. Silverside (published in Rich & Jeremy, 1998; [http://www.bsbi.org.uk/Mimulus Plant Crib 1998 AJS.pdf](http://www.bsbi.org.uk/Mimulus_Plant_Crib_1998_AJS.pdf)).



**Figure 3.1:** Species and hybrids of *Mimulus* section *Simiolus*. Reproduced by Lansdown (2009) from description of A.J. Silverdale in Rich & Jermy (1998).

### 3.2. Species characteristics

The Monkeyflower (*Mimulus guttatus*; Figure 3.2) is a member of the Family Phrymaceae (formerly a member of Scrophulariaceae) (Beardsley & Olmstead, 2002 cited in Ivey & Carr, 2012).



**Figure 3.2:** The Monkeyflower (*Mimulus guttatus*) in a clay excavation pit near the municipality Udenhout on 12 July 2012 (Photo: R. Beringen).

In its native range *M. guttatus* can be a perennial or a facultative annual terrestrial herb depending on water availability. When water availability is high (e.g. on moist soils) the plant is mostly perennial whereas at low water availability the annual ecotype mostly occurs (Truscott *et al.*, 2008a; Elderd & Doak, 2006). The plant has an erect to ascending or recumbent stem with leafy stolons which range in height from 10 to 100 cm and sometimes up to 150 cm (Kelly *et al.*, 2008; Truscott *et al.*, 2008b). The stems may be hairless or have some hairs and can sometimes be dwarfed. When the recumbent stem occurs, roots may develop at leaf nodes. The leaves are opposite, round to oval, usually coarsely and irregularly toothed or lobed, glabrous below and densely glandular-pubescent above.



**Figure 3.3:** Inflorescence of the Monkeyflower (*Mimulus guttatus*) in the Westerpark, Amsterdam, The Netherlands (Photo: B. Odé).

The inflorescence is bright yellow and develops on a raceme, most often with five or more, 20 to 45 mm long tubular flowers that are densely glandular-pubescent and have a hairy opening. The calyx has five lobes that are much shorter than the flower. Each flower has bilateral symmetry and has two lips. The upper lip usually has two lobes and the lower lip three. The lower lip may have one large to many small red to reddish brown spots and two boss-like swellings that close the throat (USDA, 2012; Stace, 1997; Poland & Clements, 2009; Rutkowski, 1998 cited in Tokarska-Guzik & Dajdok, 2010). There are some differences between the growth forms of perennial and annual plants. Perennial plants have fewer flowers, flower later and have more branches than annuals. Perennials can be recognized by flowers occurring at the fifth or more distal nodes, while annuals can be recognized by flowers occurring at the third or more distal nodes (Baker & Diggle, 2011; Hall & Willis, 2006). The differences in flowering time causes prezygotic isolation between the ecotypes (Lowry & Willis, 2010).

### **3.3. Differences with visually similar species**

*M. guttatus* has erect stems that may or may not exhibit hairs, while *M. moschatus* has creeping stems with erect ends and sticky glandular hairs. Distinction with other species of the species complex and hybrids is very difficult. Hybrids are usually sterile. Seeds are often not well formed but some hybrids produced well formed seeds that are sterile. Nevertheless other Lamiales usually have smaller flowers, quadrangle stems, sessile leaves, or entire leaves.

### **3.4. Reproductive strategy**

The species shows sexual as well as vegetative reproduction. The perennial plants invest more in vegetative reproduction through stolons or rhizomes compared to faster developing annual plants that invest more in sexual reproduction (Van Kleunen, 2007).



## 4. Habitat description

### 4.1. Habitat characteristics

Populations of the Monkeyflower (*Mimulus guttatus*) in native areas are widely scattered across moist meadows, along streams and rivers (Grant, 1924 cited in Elderd & Doak, 2006). *M. guttatus* often colonises these riparian habitats after disturbances by flooding. These disturbances cause population sizes to fluctuate over time through extinction, recolonisation, founder effects and inbreeding allowing populations to act as a metapopulation (Vickery Jr., 1999). These metapopulation characteristics are reflected in variations in the mating system of *M. guttatus* which varies from 75% selfing to complete outcrossing (Dudash & Ritland, 1991; Ivey & Carr, 2005; Ritland & Ritland, 1989; Willis, 1993 cited in Ivey & Carr, 2012).

Table 4.1 shows the ranges of environmental factors at sites where *M. guttatus* has been recorded. However, in most publications it has not explicitly been stated whether these data relate to annual or perennial types.

The species can occur at sites with air temperatures ranging during the day from 4 to 30 °C and during the night from 4 to 23 °C (Vickery Jr., 1974). The current distribution indicates that this species tolerates lower as well as higher temperatures. Soil temperatures up to 50 °C have been recorded for sites with *M. guttatus* (Lekberg *et al.*, 2012). Although plants can survive on thermal soils with temperatures ranging from 30 to 50 °C, they do show heat stress. This stress is translated in decreased total biomass, root length and diameter and early flowering to evade drought (Bunn *et al.*, 2009). Optimal growth often occurs in moderate climates with day temperatures around 17 °C and night temperatures ranging from 4 to 17 °C (Vickery Jr., 1974).

*M. guttatus* is found on soils that range from acidic to neutral and low alkaline (Bunn & Zabinski, 2003; Hani Soliman, 1976; Sletten & Larson, 1984). These soils contain multiple trace elements which can accumulate in *M. guttatus* (Appendix 2). Among these elements are heavy metals (As, Cd, Na, Al, Co, Zn, Pb) that are potentially toxic to plants (Lowry *et al.*, 2012; Samecka-Cymerman & Kempers, 1999; Qian *et al.*, 1999). Lowry *et al.* (2012) found differences in mean accumulation of macronutrients (Ca, K, Mg, P, S), analogues of macronutrients (Rb, Sr), micronutrients (B, Co, Cu, Fe, Li, Mn, Mo, Ni, Se, Zn) and potentially toxic elements (As, Cd, Na) between coastal perennial and inland annual types of *M. guttatus* (Appendix 3).

In the native range the perennial plants mostly occur along the coast where persistent fog keeps temperatures relatively low, maintains high soil moisture and reduces plant transpiration (Hall & Willis, 2006; Lowry *et al.*, 2008; Corbin *et al.*, 2005 cited in Lowry *et al.*, 2009). In these coastal areas the plants experience a relatively high amount of salt spray, therefore the perennial plants have developed a high tolerance to salt (Table 4.1; Lowry *et al.*, 2008). The late flowering of perennials compared to annuals makes it impossible for them to survive more inland where drought stress is high due to hot summers that dry out the soil. Therefore, in inland habitats mostly drought tolerant annual plant populations occur. These populations are able to survive hot summers through early flowering and seed setting. Plants die off in the dry period but

the seeds survive and germinate in the next growing season. Annual plants are not able to survive in coastal habitats because they are not tolerant to the high salt conditions occurring with salt spray (Table 4.1; Lowry *et al.*, 2008; Wu *et al.*, 2010).

**Table 4.1:** Environmental tolerances of the Monkeyflower (*Mimulus guttatus*) in the Netherlands (this study) and abroad.

Parameter	Physiological tolerance	References
pH	3 – 7.9	Bunn & Zanbinski (2003); Hani Soliman (1976); Sletten & Larson (1984)
	6.5 – 6.8	This study
Alkalinity (eq l <sup>-1</sup> )	4.851E <sup>-4</sup> – 8.668E <sup>-4</sup>	This study
Conductivity (Micromhos cm <sup>-1</sup> at 25 °C)	491.15	Sletten & Larson (1984)
Day temperature (°C) <sup>e</sup>	4 - 30	Vickery Jr. (1974)
Night temperature (°C) <sup>e</sup>	4 - 23	Vickery Jr. (1974)
Soil Temperature (°C)	Up to 50	Lekberg <i>et al.</i> (2012)
Temperature frost damage (°C)	-6 <sup>c</sup>	Bannister (1990)
Ca/Mg ratio	0.16	Murren <i>et al.</i> (2006)
Coastal tolerance to Na <sup>+</sup> (mM)	Up to 100	Lowry <i>et al.</i> (2009)
Inland tolerance to Na <sup>+</sup> (mM)	Up to 50	Lowry <i>et al.</i> (2009)
Copper (mg kg <sup>-1</sup> DS) <sup>a,d</sup>	6549.8	Tilstone <i>et al.</i> (1997)
Cadmium (mg kg <sup>-1</sup> DS) <sup>a,d</sup>	2.35	Tilstone <i>et al.</i> (1997)
Copper (ppm)	7020	Allen & Sheppard (1971)
Zinc (ppm)	538	Allen & Sheppard (1971)
Lead (ppm)	<100	Allen & Sheppard (1971)
Nickel (ppm)	135	Allen & Sheppard (1971)
Phosphate (mg kg <sup>-1</sup> DS) <sup>d</sup>	54	Samecka-Cymerman & Kempers (1999)
Potassium (mg kg <sup>-1</sup> DS) <sup>d</sup>	100	Samecka-Cymerman & Kempers (1999)
Calcium (mg kg <sup>-1</sup> DS) <sup>d</sup>	7400	Samecka-Cymerman & Kempers (1999)
Magnesium (mg kg <sup>-1</sup> DS) <sup>d</sup>	1500	Samecka-Cymerman & Kempers (1999)
Iron (mg kg <sup>-1</sup> DS) <sup>d</sup>	300	Samecka-Cymerman & Kempers (1999)
Chromium (mg kg <sup>-1</sup> DS) <sup>d</sup>	12.4	Samecka-Cymerman & Kempers (1999)
Nickel (mg kg <sup>-1</sup> DS) <sup>d</sup>	11.4	Samecka-Cymerman & Kempers (1999)
Aluminum (mg kg <sup>-1</sup> DS) <sup>d</sup>	5400	Samecka-Cymerman & Kempers (1999)
Cobalt (mg kg <sup>-1</sup> DS) <sup>d</sup>	5.9	Samecka-Cymerman & Kempers, (1999)
Lead (mg kg <sup>-1</sup> DS) <sup>d</sup>	64	Samecka-Cymerman & Kempers (1999)
Zinc (mg kg <sup>-1</sup> DS) <sup>d</sup>	122	Samecka-Cymerman & Kempers (1999)

a: value for Copper tolerant plants; b: value for non Copper tolerant plants; c: lowest air temperature were no damage to leaves occurs; d: DS = dry soil; e: temperature range is thought to be wider.

The high salt spray tolerance in perennials is expressed in a high shoot tissue tolerance to Na<sup>+</sup> ions. The exact mechanisms of this tolerance are not completely

understood, but the general theory is that plants are able to sequester these toxic  $\text{Na}^+$  ions in their vacuoles (Zhu, 2001 cited in Lowry *et al.*, 2009). In comparison with the inland annual ecotype, the coastal perennial ecotype accumulates more  $\text{Na}^+$  ions. A possible reason for this is to achieve osmotic balance with the saline soil in coastal areas. There are no differences in osmotic stress tolerances between the two ecotypes, but it is possible that they have different mechanisms to achieve these tolerances. The inland ecotype needs to be adapted to osmotic stress caused by drought whereas the coastal one needs to be adapted to osmotic stress caused by saline soils (Lowry *et al.*, 2009). This hypothesis is supported by differences in osmotic stress tolerance mechanisms between coastal and inland ecotypes of other plants (Ben Hassine *et al.*, 2008; Hu *et al.*, 2007; Teixeira & Pereira, 2007 cited in Lowry *et al.*, 2009).

Within the native range serpentine soils occur, these are characterized by low Ca/Mg ratios (Table 4.1), drought, relatively high concentrations of heavy metals (e.g. Iron, Nickel, Chromium, Cobalt (Hughes *et al.*, 2001), and often low concentrations of Nitrogen, Potassium and Phosphorous (Brooks, 1987; Gordon & Lipman, 1926; Proctor & Woodell, 1975; Vlamis & Jenny, 1948; Walker, 1954 cited in Hughes *et al.*, 2001). *M. guttatus* is able to survive on these dry, nutrient deficient soils through phenotypic plasticity and local adaptations (Hughes *et al.*, 2001; Murren *et al.*, 2006).

The species also appears to be able to colonise the Copper contaminated soil in and around the abandoned Copperopolis mine in California (Allen & Sheppard, 1971; Macnair *et al.*, 1993). The plants on these soils are highly tolerant to Copper and also show tolerances to other heavy metals such as Zinc, Lead, Nickel (Allen & Sheppard, 1971) and Cadmium (Macnair M.R. & Cumbes O.J. unpublished data cited in Tilstone *et al.*, 1997; Table 4.1). Although Copper tolerant plants are adapted to high Copper concentrations, they are also able to establish themselves on uncontaminated soils with relatively low Copper concentrations (Harper *et al.*, 1997a,b,1998; Macnair & Watkins, 1983).

The exact physiological mechanism of Copper tolerance is still unknown for *M. guttatus*, however, there are some studies on the annual type that shed some light on its workings. Strange & Macnair (1991) found that Copper damages the cell membrane leading to greater efflux of  $\text{K}^+$  and influx of  $\text{Cu}^{2+}$  through diffusion. This suggests that it is likely that the primary Copper tolerance mechanism is located in the cell membrane. Furthermore, Robinson & Thurman (1986) found that the roots produce a Copper binding protein in response to Copper presence. The cost of Copper tolerance in tolerant plants establishing themselves on uncontaminated soils is also unknown. There are no differences in Copper requirement for vegetative growth or reproduction between the two ecotypes (Harper *et al.*, 1997a,b,1998). Furthermore, there are no differences in fitness between tolerant and non-tolerant plants on these soils, allowing low frequencies of tolerant individuals to occur in populations of non-tolerant individuals (Macnair & Watkins, 1983). In contrast to the cost and physiology, the genetics of the mechanism are identified. The tolerance is determined by a single dominant gene and the degree of tolerance is determined by hypostatic modifier genes (Smith & Macnair, 1998). The dominant gene makes the plant accumulate Copper in its roots, while the modifier genes regulate the partitioning of Copper between the

roots and shoots. The degree of tolerance increases with lower root/shoot Copper partitioning ratio's (Tilstone & Macnair, 1997).

## 4.2. Associations with other species

Within its native range *M. guttatus* can establish itself on sediment between tussocks of *Carex nudata*, which offer protection from herbivory. However, during the growing season, competition by *C. nudata* (e.g. through reducing light availability) reduces *M. guttatus*' size and reproductive capacity, thereby reducing the ability of *M. guttatus* to survive winter flooding (Levine, 2000; Levine, 1999; Levine, 2001). Moss mats can hinder *M. guttatus* establishment in riparian habitats. However, when establishment does take place the moss mats have a positive effect by hindering establishment of other (possibly competitive) plant species. Furthermore, the moss mats are capable of retaining seeds and thus serving as a seed bank (Kirkpatrick *et al.*, 2006).

The plant associations at three sites of *M. guttatus* in the Netherlands were highly dissimilar (Appendix 1).

Within the native range *M. guttatus* hybridizes with several other *Mimulus* species like: *M. nasutus*, *M. laciniatus*, *M. glaucescens* and *M. platycalyx* (Figure 3.1; Vickery Jr., 1964; Dole & Ritland, 1992). Because several reproductive barriers exist between these species, hybrids are often completely or partially sterile (Vickery Jr., 1964). In addition to these inter-species hybrids, hybrids between the annual coastal and perennial inland types of *M. guttatus* occur (Lowry *et al.*, 2008).

*M. guttatus* shows symbiosis with arbuscular mycorrhizae (Bunn & Zabinski, 2003; Bunn *et al.*, 2009). These mycorrhizae are able to decrease environmental stress by increasing the plants access to water and nutrients. In thermal soils, arbuscular mycorrhizae are able to decrease heat stress to other plant species. However *M. guttatus* does not benefit from symbiosis with arbuscular mycorrhizae on these soils (Bunn *et al.*, 2009).

In its native range *M. guttatus* has interactions with several animal species through reproduction and herbivory. The main pollinators are the Western honeybee (*Apis mellifera*), solitary bees, Bumblebees (*Bombus sp.*) (Robertson *et al.*, 1999) and a small sweat bee (*Dialictus sp.*) (Macnair & Gardner, 2000). Main herbivores are the Meadow spittlebug (*Philaenus spumarius*) (Ivey *et al.*, 2009), the Common buckeye (*Junonia coenia*) (Tindle *et al.*, 2004), grasshoppers (*Acridinae sp.*), leafhoppers (*Cicadellidae sp.*) (Elder, 2006) and larger herbivores like deer and cattle (Vickery Jr. *et al.*, 1986; Truscott *et al.*, 2008a). Viruses pose an additional threat to *M. guttatus*. The plant is susceptible to infection by the Cucumber mosaic virus, which can lead to chlorosis, characterised by a mosaic blistering and deformation of leaves (Carr *et al.*, 2003) and reduced above ground biomass, reduced flower production (Carr *et al.*, 2006).

To combat the negative effects of herbivory by the Meadow Spittlebug (*Philaenus spumarius*) (Ivey *et al.*, 2009) and Common Buckeye (*Junonia coenia*) (Tindle *et al.*, 2004) perennial *M. guttatus* plants form trichomes, hairy like structures that grow from the epidermis. The trichomes are straight and often glandular, they secrete a sticky

substance that can be harmful to herbivores. Furthermore, they are also capable of reducing light radiation and transpiration rates. However, these factors are negligible for the perennial plants since they do not experience drought and intense sunlight. The inland annual plants produce none or very few trichomes. This is because of their short life time (6-10 weeks) and exposure to minimal insect herbivory. Moreover, trichome production is costly in these water limited habitats (Holeski, 2007).

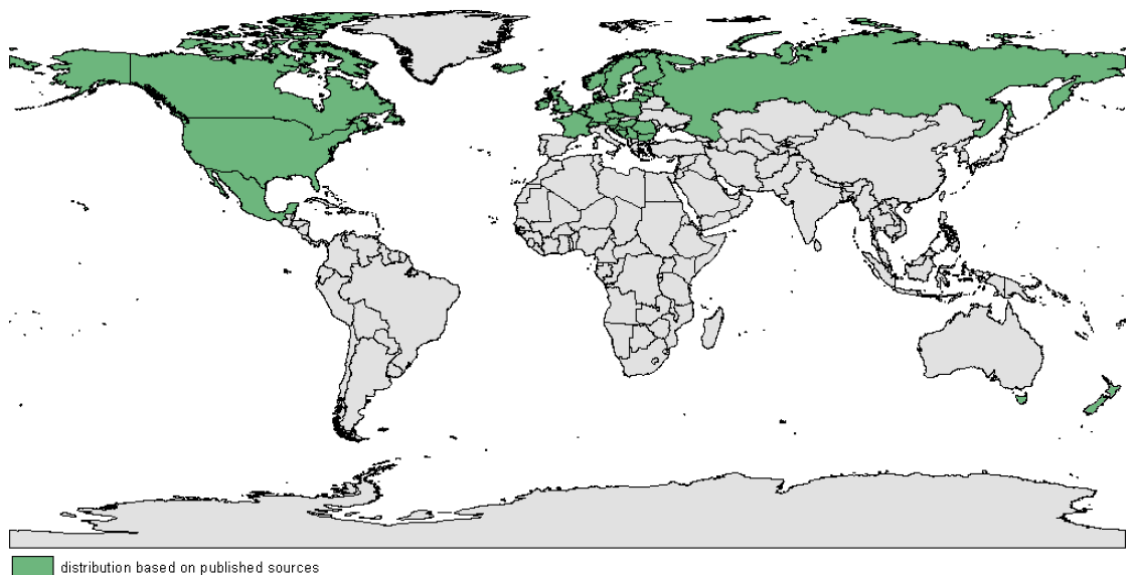
To attract pollinators the corolla has distinct regions where UV radiation is absorbed or reflected. This allows the pollinators to locate the flower and access nectar faster, thereby increasing the efficiency of pollination (Rae & Vamosi, 2012). Flower size is also an important factor in pollinator attraction since pollinators prefer larger flowers (Martin, 2004). *M. guttatus* is able to reproduce in the absence of pollinators through vegetative reproduction or by means of autofertility (Truscott *et al.*, 2006; Arathi & Kelly, 2004).

## 5. Distribution, dispersal and invasiveness

### 5.1. Global distribution

The native range of the Monkeyflower (*Mimulus guttatus*) is spread throughout the western part of North America and ranges from Alaska to Northern Mexico (Carr & Eubanks, 2002) and has an eastern boundary in Montana and South Dakota (Hegi, 1965; Hultén & Fries, 1986; Meusel *et al.*, 1978 cited in Tokarska-Guzik & Dajdok, 2010).

Figure 5.1 and table 5.1 show that *M. guttatus* has invaded multiple countries in the northern hemisphere and some countries in the southern hemisphere. The non-native range includes the eastern part of the United States and Canada, Western Europe, Russia, New Zealand and Tasmania (Vickery Jr., 1974). The figure can give a distorted image as one or few sighting may also result in the highlighting of an entire country or state.



**Figure 5.1:** Worldwide distribution of the Monkeyflower (*Mimulus guttatus*). Source: Q- bank Factsheet *M. guttatus* (Anonymous, 2012a) and additional data on distribution in Tasmania and New Zealand from Vickery Jr. (1974).

*M. guttatus* was first introduced to the United Kingdom in 1812 and had established itself in the wild by the year 1824. It is generally found in wet habitats such as streams, rivers, ponds and marshy ground (Preston *et al.*, 2002 cited in Truscott *et al.*, 2006), and flowers from June to September (Truscott *et al.*, 2006; Anonymous, 2012b). *M. guttatus* possesses several characteristics that can contribute to its invasive capabilities. These include: high seed production (Vickery Jr., 1999), relatively short germination period (Lindsay, 1964, cited in Truscott *et al.*, 2006), competitive-ruderal life history strategy (Grime *et al.*, 1988 cited in Truscott *et al.*, 2006), rapid growth (Waser *et al.*, 1982) and effective dispersal mechanisms (Vickery Jr. *et al.*, 1986). In Scotland, perennial *M. guttatus* plants often occur in discrete patches along streams with inter-population distances ranging from several meters to several kilometres (Truscott *et al.*, 2006). The largest populations are often located at the top of the

tributaries and act as source populations to the downstream areas. The presence and size of the populations along the tributary varies between years depending on winter survival and recolonisation events (Truscott *et al.*, 2006). Furthermore, the balance between survival and recolonisation assures that not all suitable habitats are invaded at the same time.

Following high flow events *M. guttatus* colonises disturbed areas of the riverbank where reduced competition from other vegetation ensures high light availability and free space. In addition to these naturally occurring substrates, *M. guttatus* is also able to establish itself on the mossy boulders of groynes which serve as ephemeral substrates and are prone to a high level of disturbance during high flows. These substrates mostly occur within one metre of the river edge, only rarely does *M. guttatus* establish itself in neighbouring habitats further up into the floodplain (Truscott *et al.*, 2008a).

**Table 5.1:** Countries where the Monkeyflower (*Mimulus guttatus*) is introduced in nature.

Country	Occurrence	References
Austria	Common	Tokarska-Guzik & Dajdok (2010)
Belgium	Local	Tokarska-Guzik & Dajdok (2010)
Czech republic	Local	Tokarska-Guzik & Dajdok (2010)
Denmark	Local	Tokarska-Guzik & Dajdok (2010)
Estonia	Rare	Tokarska-Guzik & Dajdok (2010)
Finland	Rare	Tokarska-Guzik & Dajdok (2010)
Faroe Islands	Rare	Tokarska-Guzik & Dajdok (2010)
Germany	Common	Tokarska-Guzik & Dajdok (2010)
Iceland	Rare	Tokarska-Guzik & Dajdok (2010)
Ireland	Local	Tokarska-Guzik & Dajdok (2010)
Latvia	Rare	Tokarska-Guzik & Dajdok (2010)
Lithuania	Local	Tokarska-Guzik & Dajdok (2010)
The Netherlands	Common	This study (Figure 5.2)
Norway	Local	Tokarska-Guzik & Dajdok (2010)
Poland	Local	Tokarska-Guzik & Dajdok (2010)
Sweden	Rare	Tokarska-Guzik & Dajdok (2010)
United Kingdom	Common	Vallejo-Marin (2012)
Russia	Unknown	Vickery Jr. (1974)
Eastern part of U.S.	Unknown	Vickery Jr. (1974)
Eastern part of Canada	Unknown	Vickery Jr. (1974)
New Zealand	Unknown	Vickery Jr. (1974)
Tasmania	Unknown	Vickery Jr. (1974)

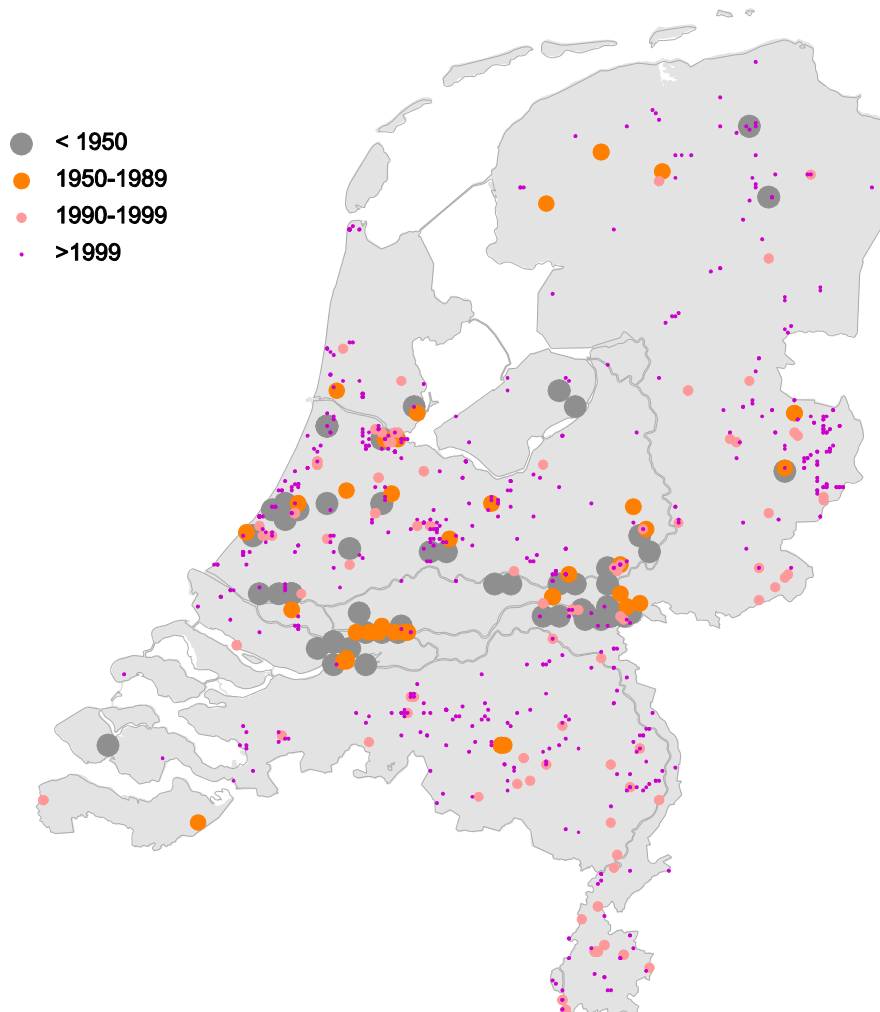
Common: many sites; Local: locally abundant, many individuals in some areas of the country; Rare: few sites.

## 5.2. Current distribution in the Netherlands

### 5.2.1 Geographical distribution and trends in range extension

The first record of *M. guttatus* in the Netherlands was in 1836 in the vicinity of Haarlem on a swampy bank of a canal (Mennema *et al.*, 1985). The geographical distribution of the species in the Netherlands is presented in figure 5.2.

In the past century, *M. guttatus* mainly occurred ephemerally in parts of floodplains that are susceptible to flooding during winter and in urban areas. At present, the species still occurs along riverbanks. Although the number of individuals is only specified in a limited number of records, it seems that the larger and persisting populations nowadays are found in kilometre squares located outside the riverine district. These large populations grow in mesotrophic, moist, low to moderate dynamic habitats, where vegetation is still in an early succession stage (possibly due to recurrent inundation in winter or recent soil disturbance).



**Figure 5.2:** Distribution of the Monkeyflower (*Mimulus guttatus*) in the Netherlands (Data: National Database Flora en Fauna, complemented with data sources mentioned in section 2.2).

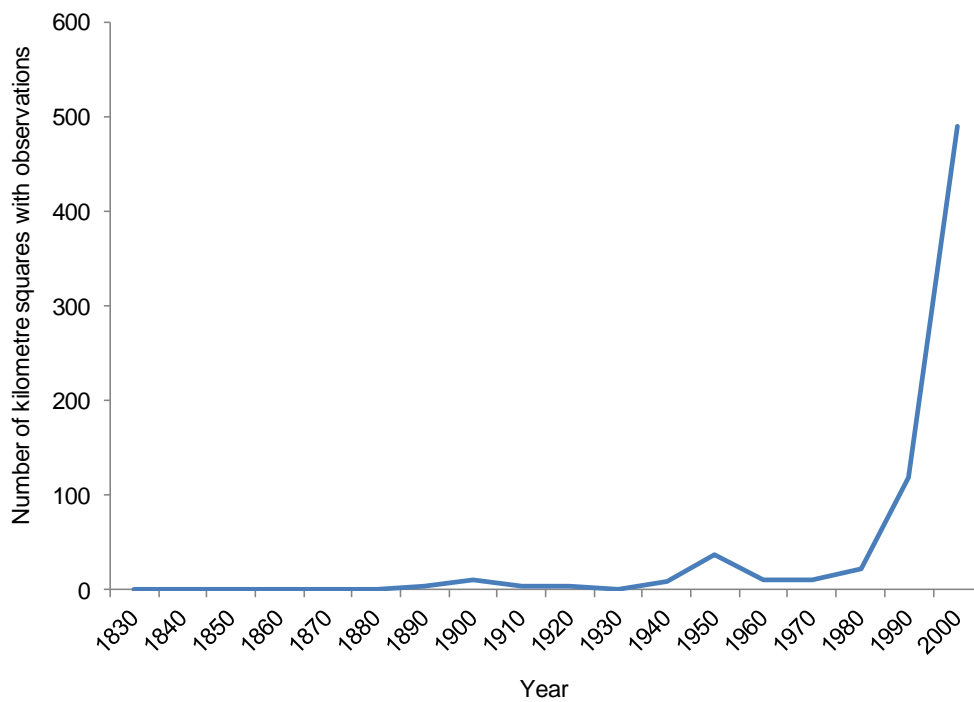
It is still unknown whether annual and / or perennial types of *M. guttatus* occur in the Netherlands. However, during the field surveys of a claypit near Udenhout (Province Noord Brabant) and a small river valley near Renkum (Province Gelderland) creeping stolons of *M. guttatus* remaining from last year were recorded (Figure 5.3). These creeping stolons are characteristic of the perennial form of the plant. These plants also exhibited poor seed setting. The plants observed at Udenhout were only seen in the riparian zone that inundates periodically. Our observations may be biased for



perennial plants because locations for our field surveys were selected using high density and occurrence during several years as selection criteria.

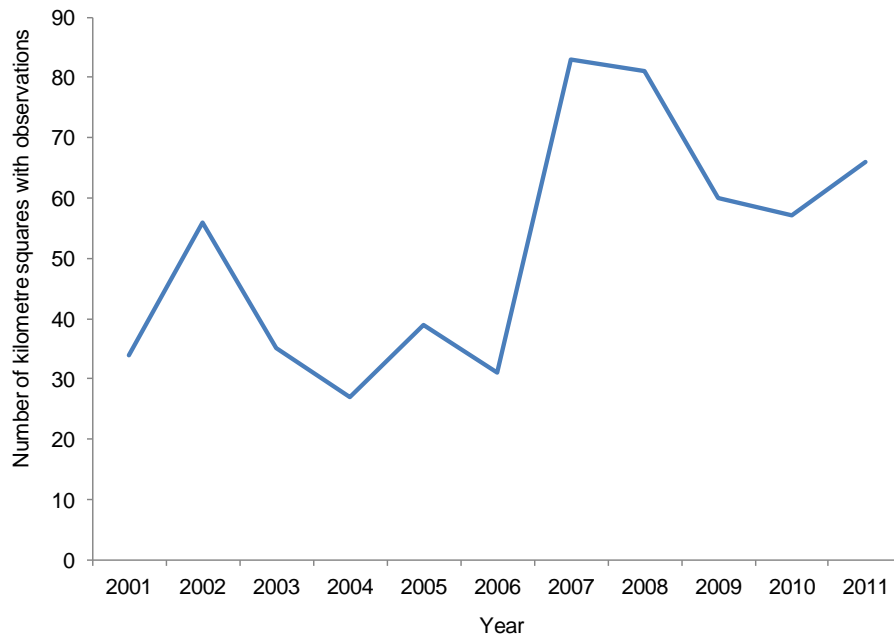


**Figure 5.3:** The Monkeyflower (*Mimulus guttatus*) with creeping stolons collected in a claypit near Udenhout, Province Noord Brabant, The Netherlands on 12 July 2012 (Photo: R. Beringen).

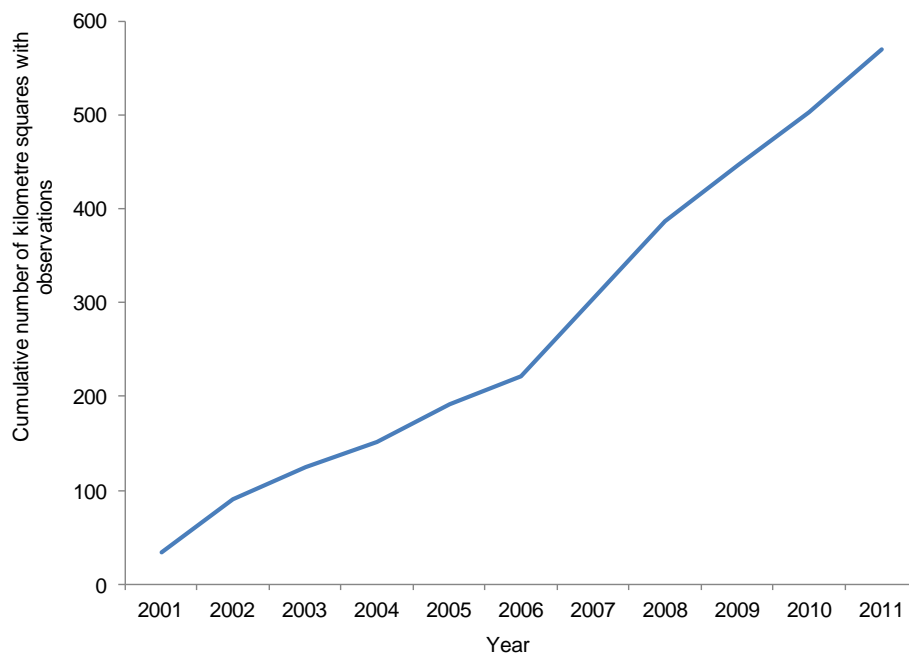


**Figure 5.4:** The number of kilometre squares where the Monkeyflower (*Mimulus guttatus*) has been observed in each decennium since the first record around 1830.

A trend analysis was carried out to gain an impression of the colonisation history and spread rate of *M. guttatus* in the Netherlands. *M. guttatus* was already recorded in the Netherlands in the 19<sup>th</sup> century, but the number of records increased rapidly since 1980s (Figure 5.4). After the year 2000, the yearly number of new records has been relatively consistent (Figures 5.5 and 5.6). The cumulative number of kilometre squares with records of *M. guttatus* shows a more or less linearly increase, suggesting that the spread of the species is still in progress (Figure 5.6).



**Figure 5.5:** The number of kilometre squares where the Monkeyflower (*Mimulus guttatus*) was observed since 2000.



**Figure 5.6:** The cumulative number of kilometre squares where the Monkeyflower (*Mimulus guttatus*) was found.

## 5.2.2. Colonisation of high conservation value habitats

Table 5.2 shows that *M. guttatus* occurs in many areas of high conservation value defined according to Annex 1 of 92/43/EEC Habitats Directive (i.e. Natura 2000 sites).

**Table 5.2:** Occurrence of the Monkeyflower (*Mimulus guttatus*) in Natura-2000 areas.

Confirmed <sup>1</sup>	Possible <sup>2</sup>
Arkemheen	<i>Achter de Voort, Agelerbroek &amp; Voltherbroek</i>
Broekvelden, Vettenbroek & Polder Stein	<i>Biesbosch</i>
Duinen Den Helder-Callantssoog	<i>Deurnsche Peel &amp; Mariapeel</i>
Gelderse Poort	<i>Dwingelderveld</i>
Kampina & Oisterwijkse Vennen	<i>Haringvliet</i>
Kennemerland-Zuid	<i>Lonnekermeer</i>
Loevestein, Pompveld & Kornsche Boezem	<i>Maasduinen</i>
Loonse en Drunense Duinen & Leemkuilen	<i>Nieuwkoopse Plassen &amp; De Haeck</i>
Meijendel & Berkheide	<i>Oude Maas</i>
Meinweg	<i>Uiterwaarden Zwarte Water en Vecht</i>
Noordhollands Duinreservaat	
Oostelijke Vechtplassen	
Polder Westzaan	
Roerdal	
Uiterwaarden Waal	
Veluwe	
Witte Veen	

1: Records with detailed coordinates and growing site within the boundaries of the Natura-2000 area; 2: Observations with a kilometre square record and Natura-2000 area within this kilometre grid.

Although only few records contain detailed information on biotopes, available data show that the species may occur in the following habitat types:

- H2190 Humid dune slacks;
- H3130 Oligotrophic to mesotrophic standing waters with vegetation (*Littorelletea uniflorae*);
- H3270 Rivers with muddy banks with *Chenopodium rubri* p.p. and *Bidention* p.p. vegetation.

The species may also occur on banks of water courses on plain levels with habitat type H3260 (*Ranunculion fluitantis* and *Callitricho-Batrachion*).

Within the abovementioned habitat-types the species grows at sites that are flooded or inundated during the winter period and dry up in summer. Therefore these sites are often scarcely vegetated (e.g., banks of brooks, ditches, fens and floodplain waters and in moist, mesotrophic grasslands). *M. guttatus* often appears on moist barren soils resulting from implementation of nature-restoration projects.

### 5.3. Pathways and vectors for dispersal

#### 5.3.1. Dispersal potential by natural means

After *M. guttatus* has been introduced it disperses via two mechanisms: seed setting and regeneration of fragmented parts. *M. guttatus* releases its seeds from August to September and mean seed numbers are found to be higher in non-native ranges. During our field surveys in the Netherlands seed setting was already recorded in early July.

In dynamic floodplains seeds are dispersed during high flow events after the initial seed setting period (e.g. in winter; Goodson *et al.*, 2002). The seeds of *M. guttatus* are buoyant after release, however, this buoyancy decreases after time. The speed at which buoyancy decreases is strongly determined by the hydrological characteristics of the river. *M. guttatus* seeds show significantly shorter buoyancy with increasing high flows and turbulence. At an average daily flow velocity of  $0.28 \text{ m s}^{-1}$  seeds can be transported for 1 km. However, some seeds retain buoyancy longer at average daily flow velocities of  $0.82 \text{ m s}^{-1}$  and were able to disperse over a distance of 3 km (Truscott *et al.*, 2006). Water only facilitates downstream dispersal, but seeds can also be dispersed upstream by wind and animals. Dispersal through wind can only occur over short distances of several meters, whereas dispersal by animals like deer, birds and cattle can disperse seeds over 1 km and possibly even further (Truscott *et al.*, 2006; Vickery Jr. *et al.*, 1986; Waser *et al.*, 1982; Lindsay, 1964 cited in Vickery Jr. *et al.*, 1986). The relative importance of seeds in long-distance dispersal is dependent on the environmental conditions in the period of seed setting.

Fragmentation can occur through rough hydrological conditions or herbivory. Fragments can have considerable regenerative capacities. Fragments of any length are capable of root extension along the main stem and from the nodes. Fragments can occur year round and survive up to 6 weeks which, in combination with high flow velocities, means that *M. guttatus* is able to disperse over very large distances throughout the year. However, long distance dispersal is often hampered by the trapping of fragments in vegetation, stones and other obstacles along the river banks (Truscott *et al.*, 2006).

#### 5.3.2. Dispersal potential with human assistance

The potential dispersal vectors of *M. guttatus* are summarized in table 5.2. *M. guttatus* is mainly used as an ornamental plant and therefore it is most likely that the species has been introduced to non-native habitats via horticulture and the ornamental plant trade (Tokarska-Guzik & Dajdok, 2010; Often *et al.*, 2003).

**Table 5.2:** Potential dispersal factors of the Monkeyflower (*Mimulus guttatus*).

<b>Vector / Mechanism</b>	<b>Mode of transport</b>	<b>Examples and relevant information</b>	<b>References</b>
Humans	Ornamental plant trade	Introduced/escaped from gardens; wildflower seeds mixtures; multiple introductions	Tokarska-Guzik & Dajdok (2010); Often <i>et al.</i> (2003); Van Kleunen & Fischer (2008)
Animals	Zoochory	Seeds in faeces of deer, cattle, birds; long distance dispersal	Truscott <i>et al.</i> (2006); Vickery Jr. <i>et al.</i> (1986); Waser <i>et al.</i> (1982)
Wind	Anemochory	Short distance dispersal	Vickery Jr. <i>et al.</i> (1986)
Water	Hydrochory	Floating seeds and fragments; short and long distance dispersal	Truscott <i>et al.</i> (2006)

It is also introduced via wildflower seed mixtures, e.g. on banks of ditches in municipality The Hague (R. Pot, unpublished observation in 2001). *M. guttatus* species was listed as a suitable species for wet and nutrient rich banks (CUR, 1994). Seed mixtures containing *M. guttatus* are still available on the Dutch market and can be ordered via internet. Potted specimens are sold by garden centres as pond plant. Our Google search for the availability of *M. guttatus* in the Netherlands revealed several sites that advertised the plant with prices ranging around €2. Some retailers mentioned that the plant was for ornamental use only and should not be introduced into nature.

#### **5.4. Invasiveness**

According to the above mentioned information it is concluded that *M. guttatus* shows a high dispersal ability in the Netherlands. The species appeared to be highly fecund and is able to disperse through active and passive means over distances > 1 km per year.

## 6. Impacts

### 6.1. Ecological effects

#### 6.1.1 Impacts on native species

##### *Adverse effects*

In Scotland, the ability of the Monkeyflower (*Mimulus guttatus*) to rapidly invade disturbed habitats can have negative effects on the species richness of the native riparian community inducing local species replacement. Here, the most striking aspect is that the coverage of *M. guttatus* in these habitats remains relatively low, mean coverage of 30% is enough to inhibit 24% of other species. Although *M. guttatus* can locally reduce species richness, it does not pose a significant threat to national species richness. Most species that are impacted are widespread ruderal plants or other non-native species and thus possess no or only low conservation value (Truscott *et al.*, 2008b). Furthermore, *M. guttatus* mostly occurs in habitats with short vegetation and high light availability. The relatively high light demand hinders its competitive ability in habitats with strongly competitive plant species such as: *Phalaris arundinacea*, *Urtica dioica*, *Chamerion angustifolium* and *Filipendula ulmaria* (Truscott *et al.*, 2008a). However, the habitat conditions in Scotland are not representative for the Netherlands (see below).

Within the Czech republic *M. guttatus* has no effect on the species richness of the communities it invades. Although it was able to achieve coverage's in the range of 30% to 40%, it does not have a serious impact on the community. The main reason for the lack of impact is that the native riparian community consists of dominant tall nitrophilous species which are far more competitive for light availability than *M. guttatus* (Hejda *et al.*, 2009).

In the United Kingdom, *M. guttatus* is known to hybridize with *M. luteus*, a species originating from South America. The hybrid is genetically isolated from the parents and is highly sterile but has been able to establish itself across the United Kingdom through vegetative regeneration. However, it was recently discovered that a hybrid population has recovered fertility through a genome duplication event, allowing it to reproduce sexually and disperse through seeds. The fertile hybrid is considered a new species named *M. perigrinus* (Vallejo-Marin, 2012).

During our field surveys in the Netherlands it has been observed that *M. guttatus* is able to establish itself in disturbed riparian habitats but is eventually overgrown, through the course of vegetation succession, by taller perennial or woody plants like Reed (*Phragmites australis*) and Willows (*Salix* sp.) (Figure 6.1).

No negative effects resulting from the influence of *M. guttatus* on native species due to parasites and diseases were discovered during the literature study.



**Figure 6.1:** The Monkeyflower (*Mimulus guttatus*) that becomes overgrown by taller Reed (*Phragmites australis*) in a stream valley near Renkum, The Netherlands, July 25, 2012 (Photo: R. Beringen).

#### *Positive effects*

No descriptions of positive effects resulting from the influence of *M. guttatus* on native species were discovered during the literature study.

### **6.1.2. Alterations to ecosystem functioning**

#### *Adverse effects*

It has been shown that the main negative impact of invasive species on native species is competition for water, light and space resource pools (Almasi, 2000; Case & Crawley, 2000; Levine *et al.*, 2003; Shea & Chesson, 2002; Woods, 1993 cited in Truscott *et al.*, 2008b). Truscott *et al.* (2008b) hypothesize that effective short and long distance dispersal methods (Truscott *et al.*, 2006) allow *M. guttatus* to rapidly colonise disturbed sediment plots. After colonisation the erect stem and rapid growth lead physical habitat changes e.g. shading of surrounding plants and also change the structural diversity of the vegetation.

Although *M. guttatus* does not pose a threat to most plant communities, a pot experiment of Baude *et al.* (2011) showed that *M. guttatus* has a higher soil nitrogen acquisition than *Lamium amplexicaule*. This higher acquisition and subsequent reduction in nutrient availability induces both direct and indirect negative effects on *L. amplexicaule* by reducing its nectar amount and quality, and floral display. These reductions might reduce attractiveness of *L. amplexicaule* to pollinators which benefits *M. guttatus* since they both compete for the same pollinators.

No information on modification of natural succession and direct disruption to food webs by *M. guttatus* was discovered during the literature study.

#### *Positive effects*

No descriptions of positive effects resulting from the influence of *M. guttatus* on ecosystem functioning were discovered during the literature study.

### **6.2. Socio-economical effects**

No socio-economical effects have been reported for Central or Northern Europe. However, *M. guttatus* is able to invade drainage ditches, which can lead to economic problems (Gudžinskas, personal observation cited in Tokarska-Guzik & Dajdok, 2010).

### **6.3. Public health effects**

According to Tokarska-Guzik & Dajdok (2010) no human health effects caused by *M. guttatus* have been recorded.



## 7. Available risk classifications

### 7.1. Formal risk assessments

Formal risk assessments of the of the Monkeyflower (*Mimulus guttatus*) have been conducted in Belgium, Ireland and the United Kingdom.

In Belgium an ecological risk assessment using the ISEIA (2009) protocol was performed, resulting in placing the species on a watch list (B2 species; score 10 points out of a maximum of 12 points; Baus *et al.*, 2010).

In Ireland a risk assessment for the hybrid: *M. x robertsii* was performed according to the Invasive Species Ireland Risk Assessment method, which resulted in a low risk score of 10 (Anonymous, 2007).

In the United Kingdom, Natural England carried out an assessment using a rapid screening process designed to be applicable to larger numbers of plants (Horizon scanning). *Mimulus cupreus x guttatus (M. x burnetii)*, a hybrid of *M. guttatus*, was characterised as low risk requiring no further assessment (Natural England, 2011).

### 7.2. Other risk classifications

Tokarska-Guzik & Dajdok (2010) describes risk classifications for Poland, Estonia, Island, Norway, Denmark and Germany. However, formal risk assessment reports on *M. guttatus* in these countries are lacking or are not accessible.

In Poland *M. guttatus* was added to the list of non-native plant species and is considered invasive in some regions of the country, but not harmful (Pysek *et al.*, 2004; Tokarska-Guzik, 2005; Zajac *et al.*, 1998 cited in Tokarska-Guzik & Dajdok, 2010).

In Estonia the species is also added to the non-native species list and is not considered invasive (Tokarska-Guzik & Dajdok, 2010).

Uncertainties exist in Iceland. It is not certain if *M. guttatus* or a hybrid of *M. guttatus* (possibly: *M. cupreus x M. nummularius x M. guttatus*) occurs along ditches and streams. However, the plants that have colonised these habitats are considered invasive (Tokarska-Guzik & Dajdok, 2010).

The slow spread of *Mimulus* species in Norway is not considered to be a problematic invasion (Tokarska-Guzik & Dajdok, 2010).

In Denmark and Germany *M. guttatus* has received the status of an established plant but is not considered invasive (Tokarska-Guzik & Dajdok, 2010).

## 8. Management options

Combating the introduction of invasive plant species involves a number of stages that should be applied in order. The first stage is to prevent the spread of the species crossing borders. The second stage is the prevention of release to the freshwater system from isolated locations such as garden ponds, by accident or deliberately. The third stage is prevention of dispersal through connected waterways and overland via vectors from the site of introduction. There is very limited information available on management measures designed specifically for the Monkeyflower (*Mimulus guttatus*), however, the following general management strategies maybe applied.

### 8.1. Prevention

Prevention should focus on the plant trade, since this is the main distribution channel. *M. guttatus* produces seeds that easily disperse autonomously, therefore dispersal out of introduced areas cannot be prevented. Caution is needed when using mechanical control measures, they can stimulate spread either by losing fragments which float away and root elsewhere, or by capturing seeds in the machinery which are subsequently released at the next area to be worked (Strykstra *et al.*, 1997).

### 8.2. Eradication and control measures

#### *Mechanical control*

There is no experience with species-specific eradication or control measures for *M. guttatus*. According to the species fact sheet from Q bank the plant is easily removable through mechanical measures (e.g. mowing), although attention must be paid to the presence of a seed bank (Anonymous, 2012a). The best option for eradication or control is mowing before ripening of the seeds. In the Netherlands the ripening of seeds has already been observed in early July. Therefore, mowing before July is advised. If done before July, the plants do not produce ripe seeds and will vanish in the long run. In the presence of upstream source populations, reducing dispersal to downstream areas is essential for effective control (Truscott *et al.*, 2008a).

For mechanical control, several machine types are available for cutting and collecting plant material (Wade, 1990; Wijnhoven & Niemeijer, 1995):

- Rotary, reciprocating and flail cutters provide an important range of machines for cutting above water vegetation. Reciprocating cutters are even useful for cutting under water. On wet soil and marshlands near the water lightweight machinery is essential. By direct collecting the cut material both seeds and minerals are removed from the sites resulting in reduced growth of all species.
- Flail cutters are not applicable for submerged aquatic vegetation, but they are the most cost efficient in terrestrial environment. They need powerful drive and therefore can only be operated by heavy machines driving on solid ground.

- Suction gear. This gear can be applied as an extension to flail cutters. The cut biomass is collected by a large vacuum cleaner like apparatus which is connected to the cutting housing. This results in the very effective collection of vegetative parts of the plants and seeds.
- Manual collecting of plants is a laborious control method, but also the most precise. In addition to large scale mechanical harvesting, manual handpicking the remaining fragments of the target species may be very effective in attempts to eradicate pest species and prevent spread, at least locally.

It is expected that mowing will not be an effective control measure for perennial plants. If the plants appear to be perennial or hybrids no management at all and allowing vegetation succession to overgrow the plants is the next best option to reduce the population size.

#### *Chemical control*

A study by Champion *et al.* (2008) showed that the herbicide triclopyrtriethylamine is lethal to *M. guttatus*. In New Zealand triclopyrtriethylamine is a registered herbicide for aquatic weed control. The active compound is relatively selective and does not cause damage to grasses, sedges, rushes and several aquatic plant species. In the past it has been used to control several aquatic species (Anonymous, 2004; Hofstra *et al.*, 2006; Sprecher & Stewart, 1995 cited in Champion *et al.*, 2008), however, no data on the use of triclopyrtriethylamine to eliminate *M. guttatus* in the field exists. Since the withdrawal of all herbicides for use in aquatic environments in the Netherlands there is no appropriate chemical method of control for these plants.

#### *Biological control*

In addition to mechanical and chemical control measures, biological measures can be used. Several herbivorous mammals, such as cows, horses or goats, can be used to control terrestrial plants. None of these have specific preferences and are therefore only practical in the control of superfluous vegetation. Plant-animal interactions are mostly the same in the non-native range compared to the native range. The same species occur within the non-native range indicating that *M. guttatus* is prone to herbivory by insects and large herbivores like deer (*Capreolus capreolus*) and cattle (*Bovidae* spp.). Sheep (*Ovis aries*), however, do not feed on the plant (Truscott *et al.*, 2008a). In addition to herbivores, the plants can be pollinated by similar pollinators as in the native range (Baude *et al.*, 2011). Classical biological control agents act specifically and usually are recruited from the area where the target species is native. Introduction of such agents is in itself a potential pest risk, and is only suitable after thorough testing.

### **8.3. Ecosystem based management**

Ecosystem based control can be focussed on intervening in the availability of natural resources such as light, water or nutrients. Reduction of nutrient availability is often achieved by exhausting the soil through repeated cutting and subsequent removal of biomass.

In the Netherlands, *M. guttatus* is able to establish itself on disturbed riparian habitats but is eventually overgrown, through the course of vegetation succession, by taller perennial or woody plants like Reed (*Phragmites australis*) and Willows (*Salix* sp.). Therefore, it is likely that the population will also reduce if no management is performed at all.

## 9. Conclusions and recommendations

### 9.1. Conclusions

In the Netherlands the Monkeyflower (*Mimulus guttatus*) appeared to be highly fecund and is able to disperse through active and passive means over distances > 1 km per year.

In the Netherlands *M. guttatus* already occurs in many areas of high conservation value, such as Natura 2000 areas.

The impacts on native species in countries outside the Netherlands have been varied. The largest effect was seen in Scotland where negative effects on the species richness of the native riparian community inducing local species replacement was observed. However, most species that are impacted are widespread ruderal plants or other non-native species and thus possess no or only low conservation value. Furthermore, in other countries effects on species richness have been minimal.

The relatively high light demand of *M. guttatus* hinders its competitive ability in habitats with strongly competitive plant species. In the Netherlands, *M. guttatus* is able to establish itself on disturbed riparian habitats but is eventually overgrown, through the course of vegetation succession, by taller perennial or woody plants like Reed (*Phragmites australis*) and Willows (*Salix* sp.).

### 9.2. Effective management options

There is no experience with species-specific eradication or control measures. Cutting of the vegetation is a way to reduce reproduction, but best timing should be experienced. The best period for mowing seems to be before July because ripening of seeds has been observed in the Netherlands in early July. If the plants appear to be perennial or hybrids no management at all and allowing vegetation succession to overgrow the plants is the next best option to reduce the population size.

### 9.3. Recommendations for further research

Recommendations for further research are focussed on the major gaps in knowledge for risk analysis of the species within the Dutch context:

- Which types of *M. guttatus* (i.e. the annual, self-fertilizing or perennial, vegetative reproducing type) occur in the Netherlands?
- Do hybrids of *M. guttatus* occur in the Netherlands?
- Do different types of *M. guttatus* prefer different biotopes?
- Are the annual and perennial type of *M. guttatus* exclusively related to disturbed and low dynamic conditions, respectively?

## Acknowledgements

We thank the Netherlands Food and Consumer Product Safety Authority of the Dutch (Ministry of Economic Affairs, Agriculture and Innovation) for financial support of this study (TRC/NVWA/2012/2009, order nr. 60400891). Dr. Trix Rietveld-Piepers of the Netherlands Food and Consumer Product Safety Authority (Office for Risk Assessment and Research, Invasive Alien Species Team) delivered constructive comments on an earlier draft of this report. The authors also thank Germa Verheggen for technical advice and assistance with physico-chemical analyses, Marije Orbons for delivering monitoring devices, Brabants Landschap for their permission to visit the Leemputten (Udenhout) and many volunteers for delivering their sightings to national databases.

## References

- Allen, W.R. & Sheppard, P.M., 1971. Copper tolerance in some Californian population of Monkey flower, *Mimulus guttatus*. *Proceedings of the Royal Society London Biology* 177: 177-196.
- Almasi, K.N., 2000. A non-native perennial invades a native forest. *Biological Invasions* 2: 219-230.
- Anonymous, 2004. Environmental impact statement (EIS) for permitted use of triclopyr. Washington State, Department of Ecology Publication, Water Quality Program Publication No. 04-10-018, 115 pages.
- Anonymous, 2007. Invasives Database December 2007. Invasive species Ireland, <http://invasivespeciesireland.com/toolkit/risk-assessment/>, Last accessed 13 July 2012
- Anonymous, 2012a. *Mimulus guttatus* Factsheet, Q bank. <http://www.q-bank.eu/Plants/Factsheets/Mimulus%20guttatus%20NL.pdf>. Last accessed 13 July 2012.
- Anonymous, 2012b. *Mimulus guttatus*, Q bank. <http://www.q-bank.eu/Plants/BioloMICS.aspx?-Table=Plants%20-%20Species&Rec=66&Fields=All>, Last accessed 14 July 2012.
- Arathi, H.S. & Kelly, J.K., 2004. Corolla morphology facilitates both autogamy and bumblebee pollination in *Mimulus guttatus*. *International Journal of Plant Sciences* 165: 1039-1045.
- Baker, R.L. & Diggle, P.K., 2011. Node-specific branching and heterochronic changes underlie population-level differences in *Mimulus guttatus* (Phrymaceae) shoot architecture. *American Journal of Botany* 98(12): 1924-1934.
- Bannister, P., 1990. Frost resistance of leaves of some plants growing in Dunedin, New Zealand, in winter 1987 and late autumn 1989. *New Zealand Journal of Botany* 28(3): 359-362.
- Baude, M., Leloup, J., Suchail, S., Allard, B., Benest, D., Mériguet, J., Nunan, N., Dajoz, I. & Raynaud, X., 2011. Litter inputs and plant interactions affect nectar sugar content. *Journal of Ecology* 99: 828-837.
- Baus, E., Branquart, E., Vanderhoeven, S., Van Landuyt, W., Van Rossum, F. & Verloove, F., 2010. [Http://ias.biodiversity.be/species/show/116](http://ias.biodiversity.be/species/show/116), Last accessed 21 August 2012.
- Beardsley, P.M. & Olmstead, R.G., 2002. Redefining Phrymaceae: the placement of *Mimulus*, tribe Mimuleae, and Phryma. *American Journal of Botany* 89: 1093-1102.
- Ben Hassine, A., Ghanem, M.E., Bouzid, S. & Lutts, S., 2008. An inland and a coastal population of the Mediterranean xero-halophyte species *Atriplex halimus* L. differ in their ability to accumulate proline and glycinebetaine in response to salinity and water stress. *Journal of Experimental Botany* 59: 1315-1326.
- Brooks, R.R., 1987. *In Serpentine and its vegetation*. In: T.R. Dudley (Ed.). Portland, OR: Dioscorides. 454 pages.
- Bunn, R., Lekberg, Y. & Zabinski, C., 2009. Arbuscular mycorrhizal fungi ameliorate temperature stress in thermophilic plants. *Ecology* 90(5): 1378-1388.
- Bunn, R.A. & Zabinski, C.A., 2003. Arbuscular mycorrhizae in thermal-influenced soils in Yellowstone national park. *Western North American Naturalist* 63(4): 409-415.
- Carr, D.E. & Eubanks, M.D., 2002. Inbreeding alters resistance to insect herbivory and host plant quality in *Mimulus guttatus* (Scrophulariaceae). *Evolution* 56(1): 22-30.
- Carr, D.E., Murhpy, J.F. & Eubank, M.D., 2006. Genetic variation and covariation for resistance and tolerance to Cucumber mosaic virus in *Mimulus guttatus* (Phrymaceae): a test for costs and constraints. *Heredity* 96: 29-38.
- Carr, D.E., Murphy, J.F. & Eubanks, M.D., 2003. The susceptibility and response of inbred and outbred *Mimulus guttatus* to infection by Cucumber mosaic virus. *Evolutionary Ecology*, 17: 85-103.
- Case, C.M. & Crawley, M.J., 2000. Effect of interspecific competition and herbivory and herbivory on the recruitment of an invasive alien plant: *Conyza sumatrensis*. *Biological Invasions* 2: 103-110.
- Champion, P.D., James, T.K. & Carney, E.C., 2008. Evaluation of triclopyr triethylamine for the control of wetland weeds. *New Zealand Plant Protection* 61: 374-377.
- Corbin, J.D., Thomsen, M.A., Dawson, T.E. & D'Antonio, C.M., 2005. Summer water use by California coastal prairie grasses: fog, drought, and community composition. *Oecologia* 145: 511-521.
- CUR, 1994. *Natuurvriendelijke Oevers*. Report 168, Civielttechnisch Centrum Uitvoering Research en Regelgeving, Gouda.

- Dole, J. & Ritland, K., 1992. Inbreeding depression in two *Mimulus* taxa measured by multigenerational changes in the inbreeding coefficient. *Evolution* 47: 361-373.
- Dudash, M.R. & Ritland, K., 1991. Multiple paternity and self-fertilization in relation to floral age in *Mimulus guttatus* (Scrophulariaceae). *American Journal of Botany* 78: 1746-1753.
- Elder, B.D. & Doak, D.F., 2006. Comparing the direct and community-mediated effects of disturbance on plant population dynamics: flooding, herbivory and *Mimulus guttatus*. *Journal of Ecology* 94: 656-669.
- Elder, B.D., 2006. Disturbance-mediated trophic interactions and plant performance. *Oecologia* 147: 261-271.
- Goodson, M., Gurnell, A.M., Angold, P.G. & Morrissey, I.P., 2002. Riparian seed banks along the lower River Dove, UK: their structure and ecological implications. *Geomorphology* 47: 45-60.
- Gordon, A. & Lipman, C.B., 1926. Why are serpentine and other magnesian soils infertile? *Soil Science* 22: 291-302.
- Grant, A.L., 1924. A monograph of the genus *Mimulus*. *Annals of the Missouri Botanical Garden* 11: 99-389.
- Grime, J.P., Hodgson, J.G. & Hunt, R., 1988. *Comparative plant ecology: a functional approach to common British species*. Cambridge University Press, Cambridge, 742 pages.
- Hall, M.C. & Willis, J.H., 2006. Divergent selection on flowering time contributes to local adaptation in *Mimulus guttatus* populations. *Evolution* 60(12): 2466-2477.
- Hani Soliman, M., 1976. PH-dependent heterosis of heavy metal-tolerant and non-tolerant hybrid Monkey flower *Mimulus guttatus*. *Nature* 262: 49-51.
- Harper, F.A., Smith, S.E. & Macnair, M.R., 1997a. Can an increased copper requirement in copper-tolerant *Mimulus guttatus* explain the cost of tolerance? 1. Vegetative growth, *New Phytologist* 136(3): 455-467.
- Harper, F.A., Smith, S.E. & Macnair, M.R., 1997b. Where is the cost in copper tolerance in *Mimulus guttatus*? Testing the trade-off hypothesis. *Functional Ecology* 11: 764-774.
- Harper, F.A., Smith, S.E. & Macnair, M.R., 1998. Can an increased copper requirement in copper-tolerant *Mimulus guttatus* explain the cost of tolerance? - II. Reproductive phase. *New Phytologist* 140(4): 637-654.
- Hegi, G., 1965. *Illustrierte Flora von Mittel-Europa*. Band VI, Teil 1. Carl Hanser Verlag München, 247-250.
- Hejda, M., Pyšek, P. & Jarošík, V., 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology* 97: 393-403.
- Hofstra, D.E., Champion, P.D. & Dugdale, A.M., 2006. Herbicide trials for the control of parrot's feather. *Journal of Aquatic Plant Management* 44: 13-18.
- Holeski, L.M., 2007. Within and between generation phenotypic plasticity in trichome density of *Mimulus guttatus*. *Journal of Evolutionary Biology* 20(6): 2092-2100.
- Hu, Y.C., Burucs, Z., Tucher von, S. & Schmidhalter, U., 2007. Short-term effects of drought and salinity on mineral nutrient distribution along growing leaves of maize seedlings. *Environmental and Experimental Botany* 60: 268-275.
- Hughes, R., Bachmann, K., Smirnov, N. & Macnair, M.R., 2001. The role of drought tolerance in serpentine tolerance in the *Mimulus guttatus* Fischer ex DC. Complex. *South African Journal of Science* 97: 581-586.
- Hultén, E. & Fries, M., 1986. *Atlas of North European vascular plants North of the Tropic of Cancer*. 1: xviii + 498 pp.; 2: xiv + 499-968 pp.; 3: 969-1149, Koeltz Scientific Books, Königstein.
- Ivey, C.T. & Carr, D.E., 2005. Effects of herbivory and inbreeding on the pollinators and mating system of *Mimulus guttatus* (Phrymaceae). *American Journal of Botany* 92(10): 1641-1649.
- Ivey, C.T., Carr, D.E. & Eubanks, M.D., 2009. Genetic variation and constraints on the evolution of defense against spittlebug (*Philaenus spumarius*) herbivory in *Mimulus guttatus*. *Heredity* 102: 303-311.
- Ivey, C.T. & Carr, D.E., 2012. Tests for the joint evolution of mating system and drought escape in *Mimulus*. *Annals of Botany* 109: 583-598.
- Kelly, J.K., Holeski, L.M. & Arathi, H.S., 2008. The genetic correlation between flower size and water use efficiency in monkeyflowers. *Evolutionary Ecology Research* 10(1): 147-152.
- Kirkpatrick, H.E., Bames, J.W.S. & Ossowski, B.A., 2006. Moss interference could explain the microdistributions of two species of monkey-flowers (*Mimulus*, Scrophulariaceae). *Northwest Science* 80(1): 1-8.



- Lansdown, R.V., 2009. *A Field Guide to the Riverine Plants of Britain and Ireland*, Ardeola Environmental Services, UK.
- Lekberg, Y., Roskilly, B., Hendrick, M.F., Zabinski, C.A., Barr, C.M. & Fishman, L., 2012. Phenotypic and genetic differentiation among yellow monkeyflower populations from thermal and non-thermal soils in Yellowstone National Park. *Oecologia* (in press).
- Levine, J.M., 1999. Indirect facilitation: Evidence and predictions from a riparian community. *Ecology* 80(5): 1762-1769.
- Levine, J.M., 2000. Complex interactions in a streamside plant community. *Ecology* 81(12): 3431-3444.
- Levine, J.M., 2001. Local interactions, dispersal, and native and exotic plant diversity along a California stream. *Oikos* 95: 397-408.
- Levine, J.M., Vila, M., Antonio, C.M.D., Dukes, J.S., Grigulis, K. & Lavorel, S., 2003. Mechanisms underlying the impacts of exotic plant species. *Proceedings of the Royal Society London Biology* 270: 775-781.
- Lindsay, D.W., 1964. Natural dispersal of *Mimulus guttatus*. *Proceedings of the Utah Academy of Science Arts and Letters* 41: 327-341.
- Lowry, D.B. & Willis, J.H., 2010. A widespread chromosomal inversion polymorphism contributes to a major life-history transition, local adaptation, and reproductive isolation. *PLoS Biology* 8(9): e1000500.
- Lowry, D.B., Hall, M.C., Salt, D.E. & Willis, J.H., 2009. Genetic and physiological basis of adaptive salt tolerance divergence between coastal and inland *Mimulus guttatus*. *New Phytologist* 183: 776-788.
- Lowry, D.B., Rockwood, R.C. & Willis, J.H., 2008. Ecological reproductive isolation of coast and inland races of *Mimulus guttatus*. *Evolution* 62(9): 2196-2214.
- Lowry, D.B., Sheng, C.C., Zhu, Z., Juenger, T.E., Lahner B, Salt, D.E. & Willis, J.H., 2012. Mapping of ionomic traits in *Mimulus guttatus* reveals Mo and Cd QTLs that colocalize with MOT1 homologues. *PLoS ONE* 7(1): e30730. doi:10.1371/journal.pone.0030730.
- Mabberley, D.J., 2008. *Mabberley's plant-book. A portable dictionary of plants, their classifications and uses*, third edition. Cambridge University Press, Cambridge.
- Macnair, M.R. & Gardner, M., 2000. Factors affecting the co-existence of the serpentine endemic *Mimulus nudatus* Curran and its presumed progenitor, *Mimulus guttatus* Fischer ex DC. *Biological Journal of Linnean Society* 69: 443-259.
- Macnair, M.R. & Watkins, A.D., 1983. The fitness of the copper tolerance gene of *Mimulus guttatus* in uncontaminated soil. *New Phytologist* 95: 133-137.
- Macnair, M.R., Smith, S.E. & Cumbes, Q.J., 1993. Heritability and distribution of variation in degree of copper tolerance in *Mimulus guttatus* at Copperopolis, California. *Heredity*, 71: 445-455.
- Martin, N.H., 2004. Flower size preferences of the honeybee (*Apis mellifera*) foraging on *Mimulus guttatus* (Scrophulariaceae). *Evolutionary Ecology Research* 6: 777-782.
- Mennema, J., Quené-Boterbrood, A.J. & Plate, C.L., 1985. Atlas van de Nederlandse Flora 2. Zeldzame en vrij zeldzame planten. Bohn, Scheltema & Holkema, Utrecht.
- Meusel, H., Jäger, E., Rauschert, S. & Weinert, E., 1978. Vergleichende Chorologie der zentraleuropäischen Flora. 2. (Karten), VEB G. Fischer Verlag, Jena, 259-421.
- Murren, C.J., Douglass, L., Gibson, A. & Dudash, M.R., 2006. Individual and combined effects of Ca/Mg ratio and water on trait expression in *Mimulus guttatus*. *Ecology* 87(10): 2591-2602.
- Natural England, 2011. *Horizon-scanning for invasive non-native plants in Great Britain*, Natural England Commissioned Report NECR053. <http://publications.naturalengland.org.uk/publication/40015?category=47020>, Last accessed 18 July 2012.
- Naturalis Biodiversity Center, 2011. Dutch Species Catalogue: Gele maskerbloem (exoot) *Mimulus guttatus*. <http://nederlandsesoorten.nl/nsr/>, Last accessed 31 July 2012.
- Often, A., Berg, T. & Stabbetorp, O., 2003. Nurseries are stepping-stones for expanding weeds [Planteskoler er springbrett for nye ugrasarter]. *Blyttia* 61: 37-47.
- Poland, J. & Clements E.J., 2009. *Vegetative key to the British Flora*. Botanical Society of the British Islands, London, Botanical Society of the British Isles, Southampton, 526 pages.
- Preston, C.D., Pearman, D.A. & Dines, T.D., 2002. *New atlas of the British and Irish flora: An atlas of the vascular plants of Britain, Ireland, the Isle of Man and the Channel Islands*. Oxford University Press, Oxford, 910 pages.
- Proctor, J. & Woodell S.R.J., 1975. The ecology of serpentine soils. *Advances in Ecological Research* 9: 255-365.

- Pyšek, P., Richardson, D. M., Rejmánek, M., Webster, G. L., Williamson, M. & Kirschner, J., 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53(1): 131-143.
- Qian, J.-H., Zayed, A., Zhu, Y.-L., Yu, M. & Terry, N., 1999. Phytoaccumulation of trace elements by wetland plants: III. Uptake and accumulation of ten trace elements by twelve plant species. *Journal of Environmental Quality* 28(5): 1448-1455.
- Rae, J.M. & Vamosi, J.C., 2012. Ultraviolet reflectance mediates pollinator visitation in *Mimulus guttatus*. *Plant Species Biology*, (in press).
- Rich, T.C.G. & Jermy, A.C., 1998. Plant Crib 1998. Botanical Society of the British Isles, London. [Plant Crib Online](#), Last accessed 18 July 2012.
- Ritland, C. & Ritland, K., 1989. Variation of sex allocation among eight taxa of the *Mimulus guttatus* species complex (Scrophulariaceae). *American Journal of Botany* 76: 1731-1739.
- Robertson, A.W., Mountjoy, C., Faulkner, B.E., Roberts, M.V. & Macnair, M.R., 1999. Bumble bee selection of *Mimulus guttatus* flowers: The effects of pollen quality and reward depletion. *Ecology* 80(8): 2594-2606.
- Robinson, N.J. & Thurman, D.A., 1986. Isolation of a copper complex and its rate of appearance in roots of *Mimulus guttatus*. *Planta* 169: 192-197.
- Rutkowski, L. (1998) *Klucz do oznaczania roślin naczyniowych Polski nizinowej*. [“Key to identification of vascular plants in lowland Poland”], Wydawnictwo Naukowe PWN, Warszawa, 812.
- Samecka-Cymerman, A. & Kempers, A.J., 1999. Bioindication of heavy metals by *Mimulus guttatus* from the Czeska Struga stream in the Karkonosze Mountains, Poland. *Bulletin of Environmental Contamination and Toxicology* 63: 65-72.
- Shea, K. & Chesson, P., 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17: 170-176.
- Silverside, A. J., 1998. *Mimulus* section *Simiolus*. Plant Crib 1998: 259-261. [Plant Crib Online](#), Last accessed 18 July 2012.
- Sletten, K.K. & Larson, G.E., 1984. Possible relationships between surface water chemistry and aquatic plants in the Northern Great Plains. *South Dakota Academy of Science Proceedings* 63: 70-76.
- Smith, S.E. & Macnair, M.R., 1998. Hypostatic modifiers cause variation in degree of copper tolerance in *Mimulus guttatus*. *Heredity* 80: 760-768.
- Sprecher, S.L. & Stewart, A.B., 1995. Triclopyr effects on peroxidase activity in target and non-target aquatic plants. *Journal of Aquatic Plant Management* 33: 43-47.
- Stace, C.A., 1997. *New flora of the British Isles*. 2<sup>nd</sup> edition, Cambridge Univ. Press, Cambridge.
- Strange, J. & Macnair, M.R., 1991. Evidence for a role for the cell-membrane in copper tolerance of *Mimulus guttatus* Fischer ex DC. *New Phytologist* 119: 383-388.
- Strykstra, R.J., Verweij, G.L. & Bakker, J.P., 1997. Seed dispersal by mowing machinery in a Dutch brook valley system. *Acta Botanica Neerlandica* 46: 387-401.
- Teixeira, J. & Pereira, S., 2007. High salinity and drought act on an organ dependent manner on potato glutamine synthetase expression and accumulation. *Environmental and Experimental Botany* 60: 121-126.
- Tilstone, G.H. & Macnair, M.R., 1997. The consequence of selection for copper tolerance on the uptake and accumulation of copper in *Mimulus guttatus*. *Annals of Botany* 80: 747-751.
- Tilstone, G.H., Macnair, M.R. & Smith, S.E., 1997. Does copper tolerance give cadmium tolerance in *Mimulus guttatus*. *Heredity* 79: 445-452.
- Tindle, J., Carr, D.E. & Eubanks, M.D., 2004. The effects of inbreeding on defense against insect herbivores, Entomological Society of America. [http://esa.confex.com/esa/2004/techprogram/paper\\_16333.htm](http://esa.confex.com/esa/2004/techprogram/paper_16333.htm), Last accessed 14 July 2012.
- Tokarska-Guzik, B., 2005. *The establishment and spread of alien plant species (kenophytes) in the flora of Poland*. Report 2372, University of Silesia, Katowice.
- Tokarska-Guzik, B. & Dajdok, Z., 2010. NOBANIS- Invasive Alien Species Fact Sheet- *Mimulus guttatus*, *Online Database of the North European and Baltic Network on Invasive Alien Species*. [http://www.nobanis.org/files/factsheets/Mimulus\\_guttatus.pdf](http://www.nobanis.org/files/factsheets/Mimulus_guttatus.pdf), Last accessed 14 July 2012.
- Truscott, A.-M., Palmer, S.C.F., Soulsby, C. & Hulme, P.E., 2008a. Assessing the vulnerability of riparian vegetation to invasion by *Mimulus guttatus*: relative importance of biotic and

- abiotic variables in determining species occurrence and abundance. *Diversity and Distributions* 14: 412-421.
- Truscott, A.-M., Soulsby, C., S.C.F., Palmer, L. Newell & Hulme, P.E., 2006. The dispersal characteristics of the invasive plant *Mimulus guttatus* and the ecological significance of increased occurrence of high-flow events. *Journal of Ecology* 94: 1080-1091.
- Truscott, A.-M., Palmer, S.C.F., Soulsby, C., Westaway, S. & Hulme P.E., 2008b. Consequences of invasion by the alien plant *Mimulus guttatus* on the-species composition and soil properties of riparian plant communities in Scotland. *Perspectives in Plant Ecology, Evolution and Systematics* 10: 231-240.
- United States Department of Agriculture (USDA), 2012. Plants database. <http://plants.usda.gov/java/profile?symbol=MIGU>, Last accessed 18 July 2012.
- Vallejo-Marin, M., 2012. Hybridization in introduced Monkeyflowers (*Mimulus*, Phrymaceae). Abstract of IWWR-Lecture June 20, 2012. Radboud University Nijmegen, Nijmegen.
- Van Kleunen, M. & Fischer, M., 2008. Adaptive rather than non-adaptive evolution of *Mimulus guttatus* in its invasive range. *Basic and Applied Ecology* 9: 213-223.
- Van Kleunen, M., 2007. Adaptive genetic differentiation in life-history traits between populations of *Mimulus guttatus* with annual and perennial life-cycles. *Evolutionary Ecology* 21: 185-199.
- Vickery Jr., R.K., 1964. Barriers to gene exchange between members of *Mimulus guttatus* complex (Scrophulariaceae). *Evolution* 18(1): 52-69.
- Vickery Jr., R.K., 1974. Growth in artificial climates - An indication of *Mimulus*' ability to invade new habitat. *Ecology* 55(4): 796-807.
- Vickery Jr., R.K., 1999. Remarkable waxing, waning, and wandering of populations of *Mimulus guttatus*: an unexpected example of global warming. *Great Basin Naturalist* 59(2): 112-126.
- Vickery Jr., R.K., Philips, D.R. & Wonsavage, P.R., 1986. Seed dispersal in *Mimulus guttatus* by wind and deer. *American Midland Naturalist* 116(1): 206-208.
- Vlamis, J. & Jenny, H., 1948. Calcium deficiency in serpentine soils as revealed by absorbent technique. *Science* 107: 549-551.
- Wade, P.M., 1990. Physical control of aquatic weeds. In: Pieterse, A. H. & Murphy, K.J., (Eds.) *Aquatic Weeds - The ecology and management of nuisance aquatic vegetation*. Oxford University Press, Oxford. 93-135.
- Walker, R.B., 1954. The ecology of serpentine soils: A symposium. II. Factors affecting plant growth on serpentine soils. *Ecology* 35: 259-266.
- Waser, N.M., Vickery Jr., R.K. & Price, M.V., 1982. Patterns of seed dispersal and population differentiation in *Mimulus guttatus*. *Evolution* 36(4): 753-761.
- Wijnhoven, A.L.J. & Niemeijer, C.M., 1995. Natuurvriendelijke oevers. In: Spijker, J.H. & Niemeijer C.M. (Eds.). *Groenwerk, Praktijkboek voor Bos Natuur en Stedelijk groen*. Instituut voor Bos- en Natuuronderzoek (IBN-DLO); Misset Uitgeverij bv Doetinchem. 521-636.
- Willis, J.H., 1993. Partial self-fertilization and inbreeding depression in two populations of *Mimulus guttatus*. *Heredity* 71: 145-154.
- Woods, K.D., 1993. Effects of invasion by *Lonicera tatarica* on herbs and tree seedlings in four New England forests. *American Midland Naturalist* 130: 62-74.
- Wu, C.A., Lowry, D.B., Nutter, L.I. & Willis, J.H., 2010. Natural variation for drought-response traits in the *Mimulus guttatus* species complex. *Oecologia* 162: 23-33.
- Zajac, A., Zajac, M. & Tokarska-Guzik, B., 1998. Kenophytes in the flora of Poland: list, status and origin. *Phytocoenosis. 10 (N.S.) Suppl. Cartogr. Geobot.* 9: 107-116.
- Zhu, J.K., 2001. Plant salt tolerance. *Trends in Plant Science* 6: 66-71.

# Appendices

## Appendix 1: Results of field surveys in 2012.

	1	2	3	
Species	<i>Mimulus guttatus</i>	<i>Mimulus guttatus</i>	<i>Mimulus guttatus</i>	
Location	Westerpark, Amsterdam	Clay pit near Udenhout	Stream valley near Renkum at edge of a former industrial area	
Date of field search	18-07-2012	12-07-2012	12-07-2012	
Amersfoort coordinates	119574-489095	140455-401296	177922-443402	
Water depth (cm)	-	2-5	2	
pH	-	6.83	6.47	
Alkalinity (meq l <sup>-1</sup> )	-	0.87	0.49	
Transparency (cm)	-	-	-	
Width (m)	-	ca. 100 m	-	
Water flow	-	-	-	
Water type	Groundwater seepage at ground level	Bank of clay pit	Wet-marshy edge of stream valley	
Surface area covered (m <sup>2</sup> )	20	2 x 100	75	
Number of individuals/shoot	75	>100	>100	
Phenology	fl/fr	fl/fr	fl/fr	
Code water sample	-	MW2	MW3	
Code sediment sample	MS1	MS2	MS3	
Code barcoding	-	C45W	C42W	
Tansley survey				
Species and growth form	Tansley score	Tansley score	Tansley score	Frequency
<i>Juncus effusus</i>	f	d	o	3
<i>Mimulus guttatus</i>	f	f	la	3
<i>Epilobium hirsutum</i>	o	r	o	3
<i>Phragmites australis</i>	a		la	2
<i>Lotus pedunculatus</i>	f	o		2
<i>Alnus glutinosa</i>	s	r		2
<i>Eupatorium cannabinum</i>	s		r	2
<i>Betula pendula</i>		f	r	2
<i>Salix cinerea</i>		f	f	2
<i>Bidens frondosa</i>		o	o	2
<i>Lycopus europaeus</i>		o	f	2
<i>Epilobium parviflorum</i>		r	r	2
<i>Equisetum palustre</i>		r	a	2
<i>Salix cf alba</i>		r	o	2
<i>Lythrum salicaria</i>	f			1
<i>Juncus articulatus</i>	f			1
<i>Rhinanthus angustifolia</i>	f			1
<i>Carex disticha</i>	lf			1
<i>Juncus subnodulosus</i>	lo			1
<i>Agrostis canina</i>	o			1
<i>Poa trivialis</i>	o			1
<i>Convolvulus sepium</i>	r			1
<i>Iris pseudacorus</i>	r			1
<i>Cardamine pratensis</i>	r			1
<i>Petasites hybridus</i>	r			1
<i>Myosotis laxa</i> subsp. <i>cespitosa</i>	r			1
<i>Eleocharis palustris</i>	r			1
<i>Angelica sylvestris</i>	s			1
<i>Prunella vulgaris</i>	s			1
<i>Filipendula vulgaris</i>	s			1
<i>Lemna minuta</i>		lf		1
<i>Myriophyllum alterniflorum</i>		lf		1
<i>Eleocharis acicularis</i>		lo		1
<i>Crassula helmsii</i>		o		1
<i>Epilobium ciliatum</i>		o		1
<i>Lysimachia vulgaris</i>		o		1
<i>Ranunculus repens</i>		o		1
<i>Apium inundatum</i>		r		1
<i>Ranunculus flammula</i>		r		1
<i>Rumex crispus</i>		s		1
<i>Agrostis spec.</i>			o	1
<i>Cirsium arvense</i>			lo	1
<i>Cirsium palustre</i>			o	1
<i>Holcus lanatus</i>			f	1
<i>Hypericum perforatum</i>			lf	1
<i>Juncus acutiflorus</i>			lf	1
<i>Populus trichocarpa</i>			s	1
<i>Solanum dulcamara</i>			r	1
<i>Tussilago farfara</i>			la	1
<i>Typha latifolium</i>			r	1
Remarks	Fragile plants max. ca. 40 cm Good seed setting	Robust plants with stolones >> 40 cm Poor seed setting Site probably temporary inundated	Robust plants with stolones >> 40 cm Poor seed setting Site probably temporary inundated	

Tansley/DAFOR score a: abundant; d: dominant; f: frequent; o: occasional; r: rare (note: prefix l was used for local). Growth form code d: floating; e: emergent; s: submerged. Phenology: fl: flowers; fr: fruits.

## Appendix 2: Accumulation capacities for different elements.

Parameter	Accumulation (mg kg <sup>-1</sup> DW)	Reference
Manganese	+/- 700	Qian <i>et al.</i> (1999)
Cadmium	+/- 1010	Qian <i>et al.</i> (1999)
Copper <sup>a</sup>	+/- 675	Qian <i>et al.</i> (1999)
Lead	+/- 260	Qian <i>et al.</i> (1999)
Nickel	+/- 330	Qian <i>et al.</i> 1999
Mercury	+/- 930	Qian <i>et al.</i> (1999)
Boron	+/- 1600	Qian <i>et al.</i> (1999)
Arsenic	+/- 35	Qian <i>et al.</i> (1999)
Selenium	+/- 409	Qian <i>et al.</i> (1999)
Nitrogen	35000	Samecka-Cymerman & Kempers (1999)
Phosphorous	1070	Samecka-Cymerman & Kempers (1999)
Potassium	30700	Samecka-Cymerman & Kempers (1999)
Calcium	1110	Samecka-Cymerman & Kempers (1999)
Magnesium	510	Samecka-Cymerman & Kempers (1999)
Iron	900	Samecka-Cymerman & Kempers (1999)
Copper <sup>a</sup>	11.3	Samecka-Cymerman & Kempers (1999)
Chromium	1.99	Samecka-Cymerman & Kempers (1999)
Nickel	1.83	Samecka-Cymerman & Kempers (1999)
Cadmium	1.21	Samecka-Cymerman & Kempers (1999)
Aluminium	248	Samecka-Cymerman & Kempers (1999)
Cobalt	3.25	Samecka-Cymerman & Kempers (1999)
Lead	10.5	Samecka-Cymerman & Kempers (1999)
Zinc	255	Samecka-Cymerman & Kempers (1999)

a = value for non Copper tolerant plants.

**Appendix 3:** Differences in accumulation between perennial and annual plants.

<b>Elements</b>	<b>Mean accumulation in coastal perennial plants (mg kg<sup>-1</sup> DW)</b>	<b>Mean accumulation in inland annual plants (mg kg<sup>-1</sup> DW)</b>
Calcium	12910	13480
Potassium	72700	61620
Magnesium	2441	2558
Phosphorous	6761	9199
Sulphur	4874	4012
Rubidium	11.25	10.8
Strontium	64.78	81.11
Boron	49.21	42.67
Cobalt	0.0383	0.0396
Copper	11.08	13
Iron	94.9	105.6
Lithium	0.2878	0.2357
Manganese	95.78	77.45
Molybdenum	4.198	16.98
Nickel	1.78	2.042
Selenium	0.0797	0.0505
Zinc	35.6	42.72
Arsenic	0.0279	0.0173
Cadmium	0.037	0.0878
Sodium	3642	1810

Source: Lowry *et al.* (2012).