

Can transgenic crops go wild?

A literature study on using plant traits
for weediness pre-screening

Suzanne P. Kos, Tom J. de Jong & Wil L.M. Tamis

Institute of Biology Leiden
Institute of Environmental Sciences



2011
COGEM Research Report: CGM 2012-01

Cover Picture: René Glas © 2011, www.reneglas.com

This report was commissioned by COGEM. The contents of this publication are the sole responsibility of the authors and do not necessarily reflect the views of COGEM.

Advisory Committee

Prof. Dr. H. van Dijk	Laboratoire Génétique et Evolution des Populations Végétales (Université Lille 1) (chairman)
F.G. Koning MSc	Netherlands Commission on Genetic Modification, COGEM (secretary)
Dr. J.E.N. Bergmans	GMO Office (Netherlands National Institute for Public Health and the Environment)
Dr.ir. L. Bastiaans	Crop and Weed Ecology (Wageningen University)
Dr. J.C.M. den Nijs	Institute of Biodiversity and Ecosystem Dynamics (IBED-UVA)
Dr.ir. J.L.C.H van Valkenburg	Netherlands Food and Consumer Product Safety Authority (Ministry of Economic Affairs, Agriculture and Innovation)

Foreword

One of the concerns about the use of genetically modified plants is the possibility of an increased aggressiveness in arable fields, their semi-natural surroundings and eventually natural ecosystems. The present report is concerned with the first step in this process: increased weediness. A thorough analysis has been made of what is known from the literature about plant characters that are presumed to enhance weediness. This knowledge was integrated in a quantifiable list of weediness traits. Application of the list to a set of plant species that can undoubtedly be classed as weeds, demonstrates the difficulties of constructing a rating system with predictive power for weediness potential. This is due principally to the finding that only a few of the candidate traits appear to be useful.

The authors have succeeded in profoundly renewing the debate about what constitute robust criteria for evaluating weediness. They have translated their choices into a quantitative questionnaire. I hope their efforts will help both applicants and evaluators to correctly interpret the aforementioned concerns.

The research was carried out by the Institutes of Biology and Environmental Sciences of Leiden University. Please note that the contents of this report do not necessarily reflect the opinion of COGEM. In an accompanying letter COGEM expresses its view on the obtained results.

Prof. Dr. Henk van Dijk (emeritus)

Contents

Summary.....	7
1. Introduction.....	9
2. Weediness according to H.G. Baker.....	13
3. Theoretical framework.....	17
4. Other literature on weediness.....	19
5. Invasiveness.....	21
6. Domestication.....	23
7. Quantification of 17 characters; the Baker+ list.....	25
8. Results.....	27
9. Assessment of selected crop species.....	31
10. Discussion and recommendations.....	33
References.....	35
Databases used.....	39
Appendix 1: WRA questionnaire.....	41
Appendix 2: Dutch questionnaire on crops.....	43

Summary

For the purposes of Environmental Risk Assessment (ERA) of Genetically Modified (GM) plants, parties applying for a license are required to provide information on whether the crop species in question can form volunteer populations on the arable field, form feral populations in disturbed semi-natural areas or even invade natural areas. A knowledge of the life-history characters that allow crops to persist and escape from the field would be very helpful in the context of ERA and accompanying evaluation. In this study we restrict ourselves to arable fields and surrounding semi-natural areas.

The first to draw up a list of weedy characters of species was the evolutionary ecologist H.G. Baker (1965). Later, Keeler (1989) claimed that with the Baker list it is possible to clearly separate crops from plants growing in the wild and from weeds. The problem is that her classification was neither objective nor well documented.

In the present study we repeated the procedure after updating the Baker list to 17 characters that can be quantified by using publicly available botanical databases. We compared 24 crops with plants from three other groups: 151 wild plants from the Netherlands, 16 plants that are considered troublesome in the Netherlands ('weeds') and 10 species from Keeler's list of the World's Worst Weeds. Crops had significantly bigger seeds and flowered and set seed during a shorter period of the year than wild plants or weeds. Crops differed especially from weeds because crops lack a persistent seed bank in the soil and have a longer vegetative period before the first flower opens. Although all these differences were significant and in the direction expected from Baker's list of weedy characters, they were gradual and there was an overlap between the respective groups. If we combine weedy characters by summation, there is no clear separation between crops, wild plants and weeds. Cross tabulation with respect to seed size and flowering period gives better separation. With the four major characters it is possible to separate crops from wild plants or weeds, but the separation is gradual and the groups still overlap. While our method may be useful for pre-screening, it provides no guarantee that a particular species will never grow wild in the Netherlands on the basis of its suite of life-history characters.

In specific cases additional factors may play a role in evaluating weediness. These factors, included in the weed risk assessment database for Australia, are whether: 1) the plant species can survive the winter, 2) it originates from a zone with a similar climate, 3) it is already a weed in other countries, and 4) the crop is highly domesticated.

Quantifying the level of domestication is at least as important as quantifying weediness. Our study also provides a checklist for quantifying domestication, because many domestication characters are opposite to Baker's weedy characters. The list can also be helpful in evaluating whether new traits of GM plants increase or decrease weediness.

A spreadsheet with all species and their scores on the measured characters is available on request from t.j.de.jong@biology.leidenuniv.nl

1 Introduction

Before a transgenic plant is allowed to be imported into or grown in the EU an Environmental Risk Assessment (ERA) is required. One of the concerns about GM plants that need to be addressed in the ERA is the persistence and invasiveness of GM crops outside cultivation. To what extent can crops produce feral populations or, in a catchier turn of phrase, 'go wild'?

In view of the current ERA procedures and the new procedures that the European Food Safety Authority (EFSA) will soon be instigating, the Netherlands Commission on Genetic Modification (COGEM) asked whether it is possible to predict which crops can go 'wild', other than by merely referring to a history of safe use in agriculture. Which plant characters are associated with 'going wild' in general? And can such characters be combined to sketch a clear profile of plants that can grow in disturbed habitats in the Netherlands. This kind of assessment tool could be useful for determining at an early stage whether a new crop has a low or high chance of 'going wild' and could be helpful for focusing attention on the latter category. With a tool like this it might also be possible to evaluate whether one or more new (GM) characteristics are likely to increase or decrease the probability of the crop 'going wild'. Finally, we apply this approach to the three crop species that COGEM considers most relevant in this context: oilseed rape, potato and apple.

The process of crops 'going wild' involves two steps; first the escape of the crop from cultivation and next the establishment of a self-sustaining population. Escaped crops are called 'volunteers' when they remain on the cultivation field and 'ferals' when they escape to semi-natural areas. Most of these escaped crops eventually disappear because they cannot form self-sustaining populations and depend on repeated introductions (Pysek *et al.* 2004a,b). Some crops can, however, form self-sustaining populations without direct intervention by humans (or despite human intervention) through recruitment of seed or clones that grow independently (Pysek *et al.* 2004a,b). After establishment, species can also spread and in some instances become invasive (Fig. 1). In general, few if any generalizations can be made about the characters that make species invasive in (semi-) natural ecosystems, perhaps because this depends to a large extent on the context (Daehler 2003). Considering that EFSA explicitly mentions that the evaluation of weediness of GM plants in production fields needs to be considered and because this is the first step in the overall process outlined in Fig.1, this study is limited to plants persisting on arable fields and spreading to semi-natural areas, thus excluding the more difficult problem of populations becoming established in more natural ecosystems. Semi-natural habitats are considered to be any habitat where human-induced changes can be discerned or which, while under human management, still has the appearance of a natural habitat in terms of species diversity and complexity (Fig. 1). In short, our focus is on ferality and volunteers.

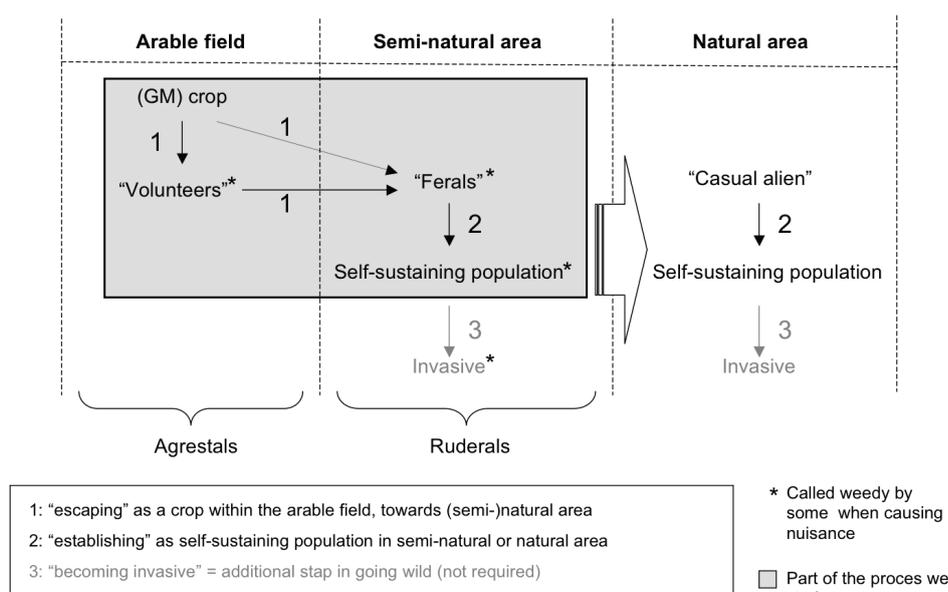


Fig. 1: Schematic display of the part of process studied here (shaded).

A weed is a plant that is considered undesirable, unattractive or troublesome by some people. One could also say it is a plant that is 'in the wrong place'. Of course, this definition depends on one's perceptions. Agriculturalists label a species weedy when it occurs in agricultural or horticultural systems and negatively affects yield, whereas conservationists will be more concerned with species inhabiting large areas of semi-natural habitat of conservation importance. Gardeners, on the other hand, may be most concerned with species that are difficult to eliminate from their gardens (Perrins *et al.* 1992a,b).

In a famous article the evolutionary ecologist H.G. Baker (1965) compared the weedy and closely related non-weedy taxa in the genera *Eupatorium* and *Ageratum* and concluded that "in both these genera similar acute differences are seen between the weedy and non weedy taxa in their reproductive biology, life form and in their various other apparent physiological features". He added that these differences are apparent in other taxa too (Baker, 1954, 1967; Adams and Baker, 1962; Cumming, 1959) and finished his article with a list of characteristics of "the ideal (?) weed". Baker (1965) defined a weed as "a plant, in any specific geographical area, of which its populations grow entirely or predominantly in situations markedly disturbed by man (without, of course, being deliberately cultivated plants)". He continued by clarifying that for him "weeds include plants which are called agrestals by some writers of floras (a plant that grows on cultivated land or among crops) as well as those which are ruderals (a plant growing and adapted to disturbed habitats, such as wasteland or roadsides)". The Baker-characteristics of 'the ideal weed' would appear to be a good starting point for our study, which attempts to quantify whether certain crops have a high or low chance of escaping into semi-natural areas. The new EFSA guidelines for ERA require that applicants list plant characters associated with weediness or invasiveness (EFSA 2010; p.41). The specific characters cited by EFSA include seed dormancy, discontinuous germination, rapid seedling growth, phenotypic plasticity, asynchronous flowering, propagule shattering, seed dispersal mechanisms and strong competitive ability (see also Warwick *et al.* 2009). As will become clear in the following chapters, the EFSA list of characters echoes Baker's ideas.

Using 16 characteristics, including all 13 characters from the Baker list, Keeler (1989) compared the world's worst weeds with non-weeds and crops and found them to have, on average, respectively 85.6%, 59.0% and 42.0% weediness characteristics. This suggests that the weediness potential of a species can be characterized by evaluating the number of weediness traits it has. Keeler (1989) observed considerable overlap between the three categories, but all the serious weeds had more than 65 percent of the weediness traits. Several people, importantly Hancock (2003), argued that this ranking scheme can aid in the identification of species with a high and low probability of becoming feral.

Unfortunately, Baker's list of characteristics is "rather vague" (Perrins *et al.* 1992a,b, Williamson 1993), and Keeler did not publish the method she used to quantify the Baker characteristics in her article. Keeler's (1989) classification of plant traits was thus subjectively based and cannot be reproduced. For instance, she classified all crops as having low seed longevity, which is questionable for several of the species listed (e.g. carrot, radish and cabbage). She also included "Reported as weed" as a separate category. Of course crops and weeds differ in this character, but used in this way it is not a predictive trait for weediness. Furthermore, she quantified her traits as categorical data (0/1 or present/absent), but since many characteristics are ordinal, with more than two categories, or vary continuously along an interval scale, this is unsatisfactory from a statistical point of view and the method can be improved. We need an approach phrased in such a way that questions can be answered objectively and reproduced independently, preferably with the use of qualitative and quantitative information from existing botanical databases.

In this study we quantified plant traits on an ordinal scale that is as precise as possible, with the aim of combining them into a single weediness measure. The simplest way to do this was to simply sum the different characters, as Keeler (1989) did, and this is the approach we have followed. Although a weighting of characters combined with more sophisticated statistical methods may yield a sharper contrast between groups, these methods were beyond the time frame available for this project. If crops have so few weediness characteristics that they fall outside the frequency distribution of the weediness measure of Dutch wild plants or that of weeds, they can be regarded as 'low-probability' for escaping cultivation and establishing in semi-natural areas. How well this method works depends on how well the groups are separated with respect to the weediness measure.

Outline. We start by detailing, discussing and quantifying the list of plant characters from the article by Baker (1965) (Chapter 2). In Chapter 3 we discuss Baker's ideas in relation to life-history theory as it emerged in the 1960s and 1970s. In Chapter 4 we review the recent literature on weediness and since some of the literature on invasiveness is relevant to our study this is briefly discussed in Chapter 5. Chapter 6 deals with domestication. Many domestication characters stand in opposition to Baker's characters, and such characters might be useful when comparing crops with their wild relatives. Other domestication characters have also been suggested in the literature. In Chapter 7 the Baker list of weedy characteristics, extended with traits derived from the modern literature, is summarized in a 'Baker+ list'.

Characters are objectively quantified using the trait values reported in existing botanical databases. In Chapter 8 we compare weedy characters for (i) a group of wild plants randomly selected from the Dutch flora, excluding trees and shrubs and plants from saline and brackish habitats, plants from stony habitats and aquatic plants. We thereby distinguish between exotic and native species, and between pioneers (codes P47 and P48 in the Standard list of the Dutch flora, Tamis *et al.* 2003) and ruderals (codes R47 and R48 in the Standard list). Pioneers grow in moist, semi nutrient-rich (P47) and moist nutrient-rich (P48) conditions. Since these conditions correspond to those on agricultural fields, we refer to this species group as *agrestals*. The *agrestals* include mostly weeds of arable crops but also pioneer plants that grow under moist (semi) nutrient-rich pioneer conditions elsewhere. Ruderals are defined here as plants of tall herb vegetation (in Dutch, “*ruigte*”), growing under semi nutrient-rich (R47) and nutrient-rich (R48) conditions. A number of other plants selected from the Dutch flora that were not in categories P47, P48, R47 or R48 of the Dutch Standard list were included in a separate category as “other wild plants”. We also included a group of (ii) crop plants that are cultivars grown on arable fields in the Netherlands. We kept separate the group of species that have both a cultivar and a wild relative (e.g. carrot, *Daucus carota*). We further distinguished (iii) a group of weeds on Dutch arable fields as selected by the COGEM guidance committee and (iv) the World’s Worst Weeds (Dutch representatives) as listed in Keeler (1989). We then addressed the following questions:

1. In which weedy characters do crops differ significantly from wild plants and from weeds?
2. By combining several characters into a single measure of weediness, can it be concluded that some crops are outside the frequency distribution of wild plants and weeds?

Finally, in Chapter 9, we take a more detailed look at three selected species; potato, oilseed rape and apple. In the discussion in Chapter 10 we evaluate how well general life-history characters predict weediness and what additional criteria one might use in a specific situation.

2 Weediness according to H.G. Baker

In his article 'Characteristics and modes of origin of weeds' published in 1965, H.G. Baker stated that:

"reproductively, the weeds are characterized by a shortness of the vegetative phase between germination and flowering, by the relative independence of environmental controls on flowering, and by an economy of pollen production associated with self-pollination. The weeds show an annual rather than a perennial habit, a wide environmental tolerance during growth, and striking developmental homeostasis (in the sense that they produce flowers and seeds successfully in a wide range of conditions). They also show plasticity in size in response to environmental variation (and, in this way, homeostasis and plasticity are not opposites)."

Box 1. Baker's (1965) list of characters of "The Ideal (?) Weed". We grouped his 14 points so that they apply to different life stages of the plants.

<p><u>1. Germination</u></p> <p>1a Germination requirements fulfilled in many environments.</p> <p>1b Discontinuous germination (internally controlled) and great longevity of seed.</p> <p><u>2. Growth</u></p> <p>2a. Shows rapid seedling growth.</p> <p>2b. Spends only a short period of time in the vegetative condition before beginning to flower.</p> <p><u>3. Fertilization</u></p> <p>3a. Self-compatible but not completely autogamous or apomictic.</p> <p>3b. When cross-pollinated, unspecialized visitors or wind-pollinated.</p> <p><u>4. Seed production</u></p> <p>4a. Continuous seed production for as long as growing conditions permit.</p> <p>4b. Very high seed output in favourable environmental circumstances.</p> <p>4c. Produces seed in a wide range of environmental conditions; tolerant and plastic.</p> <p>4d. Adaptations for short- and long-distance dispersal.</p> <p><u>5. Dispersal by vegetative means</u></p> <p>5a. If a perennial, has vigorous vegetative reproduction.</p> <p>5b. If a perennial, can regenerate from fragments.</p> <p>5c. If a perennial, has brittleness, so cannot easily be drawn from the ground.</p> <p><u>6. Biotic interactions</u></p> <p>6a. Has ability to compete interspecifically by special means (rosette, choking growth, allelochemicals)</p>

Baker concluded his article with a list of characteristics favouring weediness. This list forms the basis of the present study and is reproduced in Box 1, with the original numbering adapted to provide a clearer structure. The original listing of characteristics was considered rather vague by some, leading to potential disputes about scoring, as emphasized by Perrins *et al.* (1996a,b) and Williamson (1993). We shall first try to clarify the Baker characteristics by providing some quotes from Baker (1974), along with our interpretation and how we included the character in question in our final list:

1. Germination requirements fulfilled in many environments (1a); discontinuous germination (internally controlled) and great longevity of seed (1b).

Baker 1974:

"Most weeds are capable of maintaining in the soil a reservoir of seeds that may be triggered into germination by an appropriate stimulus (Chancellor, 1968; Holm and Miller, 1972; King, 1966; Salisbury 1961 and Wesson and Wareing 1969). By this means the weeds can take advantage of opportunities for seedling establishment that are only transiently present in some environments."

In our view a plant species that can germinate in many environments has a broad niche. We take it that discontinuous germination (internally controlled) means that seed remains dormant in unfavourable environmental conditions and can germinate immediately after the environment becomes favourable (for instance, when the soil is disturbed). Great longevity of seeds is a prerequisite for survival in the soil seed bank and waiting until a disturbance occurs. Such characters can be measured by recording whether seeds germinate at a particular time of the year or are more flexible in germination (autumn and spring) and by recording whether they have special requirements for germination like chilling, light or high temperature. The less stringent these requirements are, the more likely it is that a seed can respond by germinating immediately when conditions are favourable and does not have to wait for chilling to break dormancy. Disturbance removes competition with existing vegetation and can bring seeds closer to the surface. Both factors change the microclimate around the seed. Disturbance thus provides a window of opportunity for seedling establishment and the faster seeds germinate and seedlings establish after disturbance, the greater the chance that they can persist among perennials. Longevity of seeds can be inferred from field observations on the presence or absence of a soil seed bank.

2. Shows rapid seedling growth (2a) and spends only a short period of time in the vegetative condition before beginning to flower (2b).

Baker (1974):

"Rapid growth through the vegetative phase to the flowering condition is another feature of weeds (Baker, 1965 and 1972). This enables them to flourish in environments that are favorable for only a short time (as well as to produce more than one generation each year in those where the favorable season is more prolonged), and it also means that the necessary basis for plasticity is provided. An open habit of growth, with an early induction of flowering means not only that even tiny plants can reproduce by seed, but that when better growing conditions prevail, continuing growth (accompanied by continual production of more flowers) enables an even greater output of seeds to be achieved (Baker 1962, 1965 and 1972)."

In our view, rapid growth allows maximum capture of growth-limiting factors, such as light, water and nutrients, even in a very short time span (Basu *et al.* 2004). Grime *et al.* (1988, 2007) measured the maximum relative growth rate (R_{max} in gram per gram per week) of seedlings of many plant species. However, data on many species are still lacking. R_{max} is highly positively correlated to the specific leaf area (SLA) of plants (Poorter & Van der Werf 1998). SLA is the leaf area in mm² per mg leaf, typically evaluated under unshaded field conditions. Because SLA data are more readily available, using this trait is a good alternative for R_{max} . Milla *et al.* (2008) reviewed the extent to which SLA changes in response to environmental conditions and leaf size.

Reproduction at an early age increases the chance that a plant has already dispersed some seeds before it is killed by disturbance, which is an advantage in an unpredictable environment because it is the only way plants can reproduce before it is too late. This contrasts to the situation in a constant environment, where plants are selected to continue vegetative growth for as long as possible and then switch abruptly to flowering and seed set. In this study we estimated the age of first reproduction from the time elapsing between germination and the first flowering observed in the field.

3. Self-compatible, but not completely autogamous or apomictic (3a); when cross-pollinated, unspecialized visitors or wind-pollinated.

Baker (1974):

"A notable feature of most weeds, especially annuals, is their ability to set seed without the need for pollinator visits, either by autogamy (self-fertilization) or agamospermy (Baker, 1953, 1955, 1965, 1967 and 1972; Fryxell, 1957; Henslow, 1891; Mulligan, 1972 and Mulligan and Findley, 1972). Even when outcrossing does take place, wind or generalized flower visitors are adequate (Baker, 1965 and 1972; Mulligan, 1972 and Mulligan and Findlay, 1970). The advantages of autogamy or agamospermy for a weed include providing for starting a seed-reproducing colony from a single immigrant or regeneration of a population after weed-clearing operations have removed all but a single plant (Baker 1955 and 1965). In addition, they allow rapid build-up of the population by individuals virtually as well adapted as the founder. Where the weed is a perennial, self-compatibility is less certain to be found (and some such

weeds are even dioecious), but an extra emphasis upon vegetative reproduction here achieves the same end, i.e. the rapid multiplication of individuals with appropriate genotypes. Allard (1965) has suggested that genetic variability in a nearly completely autogamous colonizing species helps its establishment in an area being newly colonized, whereas the self-fertilization is of value in building up the adapted population from its small beginnings."

This character refers to reproductive assurance. Self-compatibility allows the plant to produce seeds even when it is growing alone. Ideal would be a plant with a high selfing rate but with some outcrossing so that it can adapt to its environment. While complete autogamy or apomixis does provide reproductive assurance, offspring will be genetically homogeneous and according to Baker will be slow to develop genetic adaptations to the local environment. Baker's reasoning makes sense, but molecular studies (summarized in Schön, Martens & van Dijk 2009) have shown that apomictic species harbour considerable genetic variation, so they can to some degree adapt to the environment. A small amount of outcrossing will allow a certain amount of genetic variation between the offspring and genetic adaptation to the local environment. Reproductive assurance might also be related to dioecy (male and female parts separated in different flowers). These male and female flowers can occur on the same individual (monoecy) or on different individuals (dioecy). In a dioecious species, seed set of females depends on the presence of a nearby male plant and such a species scores low with respect to reproductive assurance. No literature was found that showed that monoecious plants have reduced potential for seed production, and therefore only dioecious plants were given a lower score since they require two separate individuals (male and female) in order to reproduce

If a plant can only be fertilized by a single pollinator species and, vice versa, when populations of this pollinator depend heavily on this one plant species, then the pollinator may 'lag behind' when the plant species enters a new area or grows only briefly at a given site. If the plant can rely for seed set on pollinators like flies and bees that are common and visit many plant species, this would guarantee seed production.

4. Continuous seed production for as long as growing conditions permit (4a); very high seed output in favourable environmental circumstances (4b); produces seed in a wide range of environmental conditions; tolerant and plastic (4c); adaptations for short- and long-distance dispersal (4d).

Baker made no further comments on characters 4 to 6 in Box 1. In our view characteristics 4a, b and c enable the plant to produce as many seeds as possible that are dispersed both spatially and temporally into a maximum number of favourable locations to rapidly fill up the open environment. Continuous seed production can be measured as the number of months that a plant continues to flower. Seed production data can be collected from various databases. Ecological amplitude is a measure of the range of environments in which the plant can grow, i.e. the number of ecotopes for which a species is reported.

Given that terrestrial plants are not mobile, the only chance for long-distance spread is via seed or other propagules (Basu *et al.* 2004). In our view, however, the addition of short-distance dispersal to the list of traits is not useful. For short-distance dispersal the only requirement is that some seeds land on the soil adjacent to the plant and this will be the case in almost all plant species, even if all seeds are capable of long-distance dispersal. We therefore regard any adaptation for long-distance dispersal, by wind, water, birds or humans, as a weedy character.

5. If a perennial, has vigorous vegetative reproduction (5a), can regenerate from fragments (5b) and has brittleness, so cannot easily be drawn from the ground (5c).

In our view vegetative reproduction enables the plant to rapidly colonize an open environment without losing time in reproduction. When an opportunity arises, the plant quickly covers the soil around it. We collected data on whether species have vegetative growth or reproduce from a single stem.

The ability to regenerate makes the plant more tolerant to disturbance and this ability is related to the number of meristems that can be used for regrowth. Plants with strong apical dominance, resulting in an upright growth habit, generally suffer more from disturbance than plants with a prostrate growth habit because they have fewer meristems. Malíková *et al.* (2010) found that upright annuals have a smaller number of shoots and regenerate less successfully than prostrate annuals. Having meristems close to the ground also reduces the fraction of meristems lost in a disturbance like treading or mowing. We would therefore suggest that the Raunkiær life form (Müller-Dombois & Ellenberg 1974) may provide a good indication of the regenerative ability of plants, with meristems close to the soil surface reducing damage and promoting regrowth. Raunkiær classified plants based on the position of growth points (buds) during adverse conditions (winter).

Baker's concept of 'brittleness' we find rather ambiguous. If a plant breaks easily, it may be able to regenerate from the fragments produced, and brittleness is then an advantage when humans or animals try to remove it. However,

a plant that breaks easily after only minor disturbance loses more biomass than a tough and flexible plant. Because this characteristic remains rather ambiguous and is also not readily quantified, we have omitted it from our list of weediness traits.

Although characters 5a,b apply mostly to perennials, this is not exclusively so. Annuals and biennials can also exhibit limited vegetative reproduction or regeneration from fragments. We therefore dropped Baker's proviso "if a perennial" and consider how these traits apply to any plant species.

6. Has ability to compete interspecifically by special means (rosette, choking growth allelochemicals) (6a).

Competitive ability allows the plant to grow even when it is close to other plants. Grime *et al.* (1979) quantified this character, using plant height and lateral spread. In Hodgson *et al.* (1999) canopy height and lateral spread were used as a measure of competitive strength for grasses, sedges and rushes, while for other herbaceous species they used canopy height, lateral spread and leaf dry weight. We shall use canopy height from Biobase (CBS 1997) and lateral spread from the CLO-PLA database (Klimešová & Klimes 2006). Harper (1977) has questioned the role of allelochemicals and since it is unclear whether allelochemicals play any ecological role it is not useful to incorporate this trait in our list. Note that competitive ability is the odd one out on the Baker list. Traits 1-5 all allow the plant to grow maximally and occupy a highly disturbed and open environment as fast as possible when it is growing on its own. Point 6, in contrast, addresses the competition that is inevitable in later successional stages; it applies to competitive ruderals rather than to ruderal plants.

3 Theoretical framework: life-history strategies: *r*- en *K*- selection and Grime's C-S-R strategies

In 1965, when Baker wrote his article, life-history theory of plants was still in its infancy. In 1967 many of the Baker traits were summarized in the context of *r*- and *K*-selection in the book "The theory of island biogeography" by MacArthur and Wilson. Also in Grime's classification system (1979), which refers to Competition, Stress and Ruderal strategies, several of Baker's weediness characteristics resurface. Because both theories have been hugely influential in ecology and complement Baker's ideas, we summarize and discuss them here.

Baker's characters 1-4 (in our renumbering) allow plant populations to grow quickly and colonize new, open habitats. In the theory of *r* or *K* selection of MacArthur and Wilson (1967) these characters were later referred to as *r*-selected. The '*r*' refers to the intrinsic rate of natural increase of the population. A population grows each year with a factor e^r . The parameter *K*, the maximum number of individuals that can grow in a given area, refers to the carrying capacity. When the population reaches the carrying capacity it no longer increases in size. MacArthur and Wilson (1967) argued that when colonizing an island, populations are, for some time, growing. During this phase of population growth there is selection for rapid growth and short generation time (see also Lewontin 1965). When the island is full and the carrying capacity is reached, short generation times lose their benefit and density-dependent selection favours other characters like competitiveness and the total seed number produced during the plant's life. With *K*-selection the time during which seeds are produced does not matter so much for selection. The *r*-*K*-concept has been criticized, but in a rebuttal Boyce (1984) has argued that the concept is still quite useful when dealing with conditions of low densities and growing populations.

Agricultural weeds are often characterized as being *r*-selected on the assumption that frequent disturbance through tillage, herbicides or other agronomic practices keeps populations low and more often in a state of growth than in a state of decline (Booth *et al.*, 2003). In situations where density is high, traits such as large size, longevity and delayed reproduction are favoured, because they increase per capita seed production. Plants with this set of traits are '*K*-strategists' because the populations are theoretically maintained at or near the carrying capacity of the environment.

Grime (1979) characterized plants based on their ability to withstand competitors (C), stress (S) and disturbance (R).

- C-strategists maximize resource capture in undisturbed but productive habitats by increasing vegetative production and reducing allocation to reproduction.
- S-strategists are adapted to stressful, harsh environments where disturbance is rare and competition is unimportant. By reducing vegetative growth and reproduction, they maximize their survival.
- R-strategists maximize reproduction and growth and are adapted to disturbed but historically productive environments.

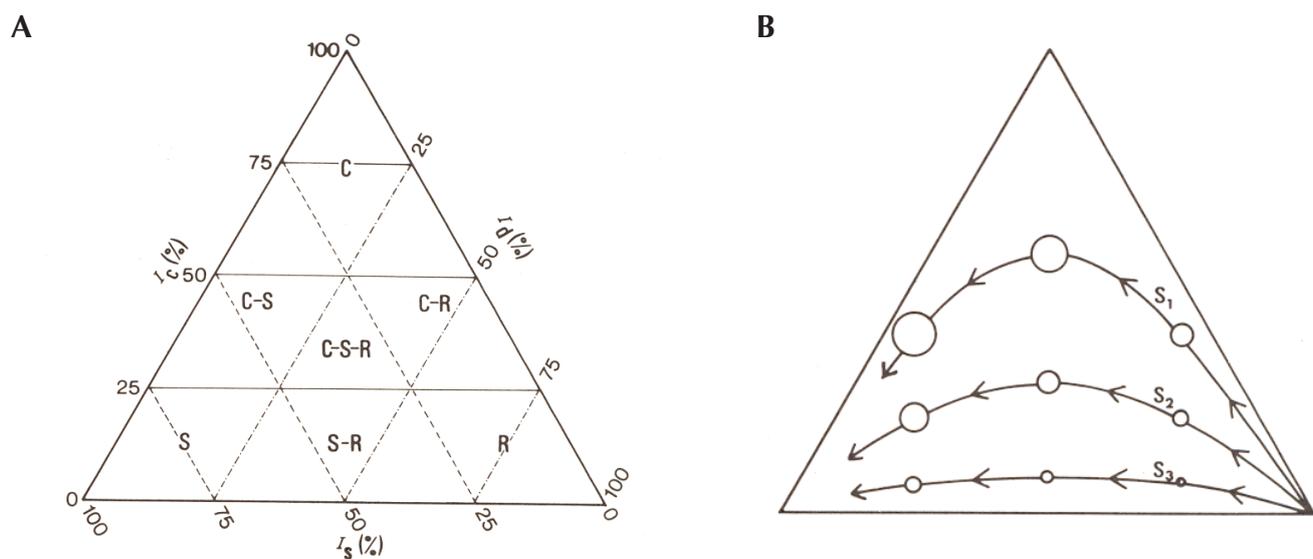


Fig. 2: (A) The C-S-R model, showing the three strategies (C= competitors, S= stress tolerators and R= disturbance-tolerant ruderals). I_c = relative importance of competition, I_s = relative importance of stress, I_d = relative importance of disturbance. (B) Diagram representing the path of vegetation succession under conditions of high (S_1), moderate (S_2) and low (S_3) potential productivity (Grime, 1979).

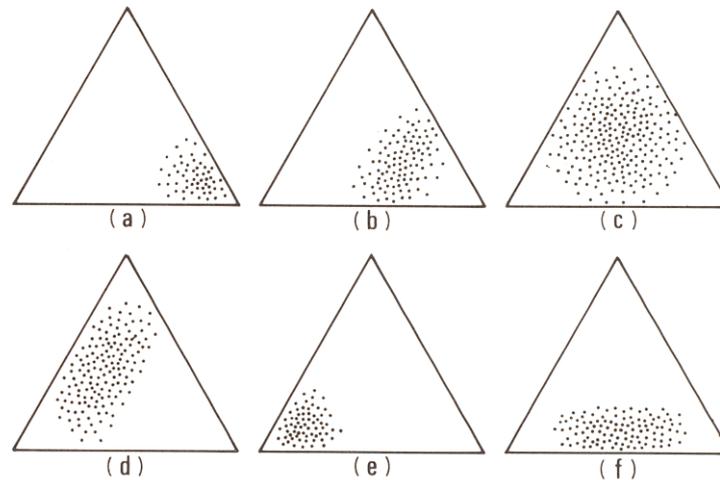


Fig. 3: Diagrams describing the range of strategies encompassed by (a) annual herbs, (b) biennial herbs, (c) perennial herbs and ferns, (d) trees and shrubs, (e) lichens and (f) bryophytes (Grime, 1979).

Grime (1979) connected his strategies to *r-K* selection by pointing out that island colonization is similar to vegetation succession. At the start of succession, ruderals (Box 2) are present. Later, competitors come into the picture, while towards the end of succession plants dominate that can withstand the stress imposed by their neighbours. In this line of reasoning, R-strategists are *r*-selected while S-strategists are *K*-selected. Grime (1979) proposed a triangular ordination in which each of the strategies is represented by one of the corners (Fig. 2A). He used the potential maximum rate of dry matter production (R_{max}) measured in a standardized productive environment and a morphology index reflecting competitive ability to place plants in the triangle (Fig. 3, Grime and Hunt, 1975).

Booth *et al.* (2003) stated that weedy species are usually classified as either ruderals (R) or competitive ruderals (CR), with CR-strategists being found in less frequently disturbed habitats than R-strategists. R-strategists fit Baker's characters 1-5, while character 6 refers to a CR strategy.

Box 2. Characterization of ruderals according to Grime *et al.* (2007, p.34), to which we have added references to the Baker list (Box 1).

- Ruderals generally:
- are herbs
 - have a small stature and limited lateral spread.
 - have a short established phase
 - have a short phase of leaf production in a period of high potential productivity
 - produce flowers already early in their life-history (Baker 2b)
 - have a high frequency of flowering (Baker 2b)
 - devote a large proportion of annual production to seeds (Baker 4b)
 - have dormant seeds (Baker 1b)
 - have regenerative strategies: seasonal regeneration in vegetation gaps, numerous small wind-dispersed seeds and spores, and a persistent seed bank (Baker 1, 4, 5)
 - have a high Relative Growth Rate, rapid curtailment of vegetative growth, diversion of resources into flowering (Baker 2)
 - have an opportunistic uptake of mineral nutrients and photosynthesis, coinciding with vegetative growth (Baker 4b)
 - do not store photosynthate and mineral nutrients in vegetative parts but confine these to seeds

4 Other literature on weediness

In order to identify any additional characteristics that might be important for weediness we first summarize and comment on the literature that appeared after Baker's publications. For each characteristic we describe whether or not we include it in our list of weediness characteristics.

When Keeler (1989) compared the distribution of the Baker characteristics among 'the world's worst weeds', non-weeds and crops, she added two characteristics to Baker's original list. The first was "previous reports of weediness". While the weeds obviously all score 1 on this character, it does not refer to any mechanism that *makes* these plants weedy. Previous reports of weediness may be very useful, but not in this context. Second, Keeler (1989) added polyploidy, noting that relatively many weeds and crops are polyploid as compared with a random sample from the British flora. We discuss polyploidy in Chapter 5.

Taking a sample of 49 British annuals, Perrins *et al.* (1992a,b) investigated which characteristics discriminate between weedy and non-weedy species and set out to quantify Baker's criteria. They reduced the Baker list to eight criteria (Table 1) that applied to annuals and could be scored, mostly on the basis of Grime *et al.* (1988). There are several problems with their approach. First, what constitutes a weed was determined by "the views held by the different groups (including agriculturalists, ecologists, taxonomists, conservationists and gardeners)". What counts as a weed on one person's criteria, however, may not be a weed for somebody else. Second, the group of British annuals constitutes only a limited subsample of the flora. Weedy characters may be more recognizable in a broader context that includes other life histories and crops. There was only a weak correlation between the Baker score and weediness (Williamson & Fitter 1996). In view of this limited success Perrins *et al.* (1992a) drew up a list of 19 quantitative characters that are loosely related to the Baker list in Table 1. They found only 3 of these characters to differ between weeds and non-weeds. Weeds germinate more in spring than in autumn (not directly related to the Baker list), continue to flower longer until September-October (Baker 4a) and are more likely to pass through the gut of animals (a character associated with fleshy fruits and long-distance dispersal, Baker 4d). Most seeds are formed in summer and we can well imagine that germination at the first occasion (autumn) reflects no ability to form a seedbank, whereas seeds that survive through winter and germinate in spring do have this ability. In this case autumn/spring germination corresponds to having a seedbank in the soil (Baker 1b). As acknowledged by Perrins *et al.* (1992a,b), the relation of the measured characteristics to Baker's characters is often problematic. Both Perrins *et al.* (1992a,b) and Williamson (1993) question the validity of using Baker's characters to predict weediness. While this critique follows logically from their data set and methods, it is still quite possible that when more precisely measured and applied to a broader dataset (as in Keeler 1989) Baker's method will be useful. Perrins *et al.* (1992a,b) emphasized that comparative studies between related species pairs, one weedy and one non-weedy species, are the best way forward. This is indeed a good suggestion that may also apply to a comparison of crops and their wild relatives.

Table 1. Eight weediness characters as scored as absent (0) or present (1) by Perrins *et al.* 1992b.

Code*	Criteria by which the species were scored
1a	No chilling or specific light requirements needed to break dormancy
1b	Seed bank type 3 or 4
2a	Relative growth rate of seedling at least 1.9 per week
3a	Not exclusively inbreeding or outbreeding
3b	Uses wind or a range of insects as pollinators
4a, 5b	Not all meristems devoted to flowering
4b	An average of more than 2500 seeds per plant
4d	Seed dispersal by passage through gut or attached means

* Code follows that in Chapters 2 and 7.

The 'Weed Risk Assessment' (WRA) process was developed in Australia by Pheloung *et al.* (1999), amongst others. WRA is a risk analysis tool for determining the weed potential of proposed new plant imports into Australia. Gordon *et al.* (2008) investigated the accuracy of the WRA for other countries, by applying the system to known invaders and non-invaders. The system correctly rejected 90% of the important invasive plants, but made an error in accepting them in 10% of the cases. The system correctly concluded that the non-invasive plants were harmless in 70% of the cases, but still rejected 30% of them. There may thus be certain potentially costly errors, in the sense that several invaders are allowed into the country but also that harmless plants that may have some economic value are sometimes rejected. In addition to Baker's characteristics, the possible nuisance the plant might cause and historical and geographical characteristics are included in the WRA (Appendix 1). Newly added characteristics are how widely the plant species is distributed in its native area, climate match and whether it has ever naturalized after introduction. The wide distribution is somewhat similar to Baker 4c. The other two points may be very useful in a specific situation, but do not explain what causes weediness in some species and not in others.

Table 2. Correct decisions and errors made by the WRA when evaluating known major invaders and non-invaders for different countries (Gordon *et al.* 2008)

	Reject	Accept
Major invaders	90%	10%*
Non-invaders	30%	70%

*: The shaded areas represent a wrong decision

5 Invasiveness

In this chapter we briefly review the recent literature on invasiveness and how this literature leads to the addition of extra characters to the weediness list. A full review of the literature is beyond the scope of this study, but the results of studies by Williamson and Fitter (1996), Rejmánek (2000) and Speek *et al.* (2011) are included here because some of their results apply to weediness as well.

Williamson and Fitter (1996) found that native and exotic, invasive species differ in certain characteristics. With respect to Raunkiær life form, invasive species contained less phanerophytes with buds 25 cm or more above the soil surface (compare Baker 5b), were taller in absolute length and as compared with their width (Baker 6a), had larger leaves (we will include leaf area per unit weight as Baker 2a), reproduced more often in the first year (Baker 2b) and were more often insect-pollinated and hermaphrodite (Baker 3). All these differences between invaders and native plants were significant at the 5% level but there was also considerable overlap between groups. These trends go in the same direction as suggested by the Baker list.

Speek *et al.* (2011) compared traits relating to the frequency of occurrence within the Netherlands and the frequency of dominance locally (in 1–100 m² quadrants) of exotic plant species established in The Netherlands. The model that used plant traits to explain regional frequency of exotic plant species differed from the models that best explained their frequency of local dominance. Regionally, the factors that were associated with frequency were Raunkiær life form, height (Baker 6a), polyploidy, human use and length of flowering season (Baker 4a); we already discussed these factors. The factors that correlated to frequency of local dominance were: lateral vegetative spread (Baker 5a) and residence time.

Rejmánek (2000) summarized the major predictions made by the emerging theory of plant invasiveness based on biological characters in the following ten points:

- **Relatively constant fitness** over a range of environments (Baker 4c).
- **Small genome size.** This character may be correlated with short minimum generation time, small seed size, high leaf area ratio and high relative growth rate of seedlings (Rejmánek 1996a, 1999; Bennett *et al.* 1998; Grotkopp *et al.* 1998). Contrary to the claim of Rejmánek (2000) that organisms with small genomes are good invaders, a recent publication by Pandit, Poccock & Kunin (2011) emphasized that invasive plants generally have high chromosome numbers and are polyploid. Also crops are often polyploid. We examined information in the Kew database on DNA content. This information turned out to be incomplete and sometimes unreliable. Also there seems to be no clear mechanism connecting DNA content and weediness (B. Zonneveld, personal communication, 2011). We therefore refrained from using this information.
- **Small seed mass.** Invasiveness of woody species in disturbed landscapes is associated with small seed mass (<50 mg), relatively short juvenile period (<10 years) and short intervals between large seed crops (1–4 years) (Rejmánek & Richardson 1996). These authors argued that small seeds disperse better and the effect is also indirect, through a trade-off with seed number, high germination rate, a shorter chilling period to overcome dormancy and higher relative growth rate of seedlings. Other authors have argued that, in general, small seeds more readily enter the soil, where they form a seed bank, and that small seed size is an adaptation to disturbed conditions (Baskin & Baskin 2003). We include seed size in our list under 4e, with small seeds being a weedy character (see also point 10).
- **Seed dispersal.** Vertebrate dispersal is responsible for the success of many invaders in disturbed as well as 'undisturbed' habitats (Binggeli 1996; Rejmánek & Richardson 1996; Rejmánek 1996b; Baker 4e).
- **Size of geographical range.** The size of primary (native) geographical ranges of herbaceous species apparently predicts their invasiveness (Forcella & Wood 1984; Rejmánek 1995, 1996a, 1999; Goodin *et al.* 1998). We measure the number of ecotypes of a species (Baker 4c), which might be positively related to range size.
- **Vegetative reproduction.** An important character according to Auld *et al.* (1983), Pieterse & Murphy (1990), Henderson (1991) and Aptekar & Rejmánek (2000).
 - This is Baker 5a in our list.
- **Related aliens.** Alien species belonging to exotic genera (and therefore probably possessing traits different from those of the resident species) are more likely to be invasive than are alien species with native congeners (Darwin 1859; Rejmánek 1999). This is now known as Darwin's naturalization hypothesis (Schaefer *et al.* 2011). It is not included in our list because it is context-specific and not a general weediness character.
- **Required mutualism.** Plant species depending on non-specific mutualisms are more likely to overcome abiotic

and biotic barriers in new environments (Baker 1974; Richardson *et al.* 2000). Parasites are also unlikely invaders. Specialized pollinators are covered by Baker 3b. Other mutualisms, like root symbionts, will not be added to the Baker+ list because of lack of information.

- **Habitat.** Undisturbed (natural and semi-natural) plant communities in dry environments are more likely to be invaded by tall plant species (Egler 1983; Gaudet & Keddy 1988; Pysek *et al.* 1995; Crawley *et al.* 1996; Williamson & Fitter 1996). As our study is restricted to disturbed habitats, this is not relevant here.
- **Human use.** The spread of many alien species is heavily dependent on human activity (Panetta & Scanlan 1995), especially large volumes of soil being moved around (topsoil, mud on cars, horticultural stock). Species with numerous, relatively small, seed bank-forming seeds are pre-adapted for this type of dispersal (UCPE 1996; Hodkinson & Thompson 1997). These seed characters are included as Baker 1b and 4e.

Together these studies on invasive plants led to two additions to Baker's list: seed size (4e) and whether or not a plant species is parasitic (6b).

6 Domestication

When crops are domesticated they are selected for characteristics that, in general, reduce the weedy characteristics. Warwick and Stewart (2005) drew up a list of domestication traits by which domesticated plants differ from weeds or invasive plants. This list is reproduced below. Characters 1-14 stand in opposition to Baker's characteristics and relate directly to our list. Such characters can be used when comparing, within a species, the crop to its wild relative. Wild and cultivated varieties of the same species could then have different scores on the Baker list.

1. Loss of germination inhibitors
2. Synchrony in germination (loss of secondary dormancy)
3. Narrow germination requirements
4. Short-lived seeds (no or transient seed bank)
5. Synchrony of flowering and fruit development
6. More determinate growth instead of continuous seed production
7. Increase in seed and/or fruit size and uniformity in size
8. Smaller numbers of larger fruits or inflorescences
9. Seed production high in a uniform optimal environment
10. Reduction in seed dispersal (shattering)
11. No special adaptations for seed dispersal over both short and long distances
12. Increase in apical dominance and reduced plasticity of growth
13. Reduced competitive ability
14. Selfing and/or self-incompatible (could be apomict or obligate selfer)

Warwick and Stewart (2005) mention as additional domestication traits:

15. Increase in starch, sugar or oil and decrease in protein content of the seed and/or fruit
16. Loss of bitter substances in the seed and/or fruit

7 Quantification of 17 characters; the Baker+ list

From the evaluation of Baker's publications and other relevant literature, reviewed above, we obtain the following list of characters and methods for their quantification, whereby more weedy characters score higher. The databases used are indicated in brackets; the full references are provided at the end of the main report. Information on the ecological amplitude of crops is non-existent and was subjectively entered by the authors, based on the perceived ability of the crop to grow under different conditions. As noted in Chapter 2, in questions 5a and 5b we dropped Baker's "if perennial".

1. Germination

- 1a Germination requirements fulfilled in many environments
 - 1a1 Do the seeds germinate in spring, autumn or both? (BioBase and Ecoflora)
either = 0, both = 1
 - 1a2 Are special requirements needed, like chilling (vernalization)? (Ecoflora)
Absolute requirement of either chilling (vernalization), light or temperature fluctuation for germination = 0,
Partial requirement of chilling. Either no or partial requirement of light and fluctuating temperature (or no data available) = 1/2,
No requirement of chilling. Either no or partial requirement of light and fluctuating temperature (or no data available) = 1
- 1b Seedbank
 - Seedbank (Standard list of the Dutch Flora, Tamis *et al.* 2003)
None = 0,
Transient (seeds surviving less than 1 year) = 1/3,
Short-term (seeds surviving 1–4 years) = 2/3
Long-term persistent (seeds surviving for > 4 years in the soil) = 1

2. Growth

- 2a. Shows rapid seedling growth
 - Specific Leaf Area in mm²/mg (LEDA, Kleyer *et al.* 2008)
Less than 18 mm²/mg = 0
Between 18 and 22.0 mm²/mg = 1/3
Between 22.1 and 30.0 mm²/mg = 2/3
More than 30.1 mm²/mg = 1
- 2b. Spends only a short period of time in a vegetative condition before beginning to flower
 - Months vegetative: month of flowering – month of germination (BioBase)
<1 month = 1
2-3 months = 4/5
4-5 months = 3/5
6-11 months = 2/5
12-24 months = 1/5
>25 months = 0

3. Fertilization

- 3a+b. Self-compatible but not completely autogamous or apomictic (BioBase)
Self-compatible = 1
Completely apomictic = 3/4,
Cross-pollinated by unspecialized visitors or wind-pollinated (BioBase, Ecoflora)
Unspecialized visitors = 1/2
Specialized visitors = 0
- 3c Sex system (BioBase)
Hermaphrodite (male and female in one flower) = 1
Monoecious (male and female flowers on a plant) = 1
Dioecious (male and female flowers on different plants) = 0

4. Seed production

- 4a. Continuous seed production for as long as growing conditions permit (LEDA and BioBase)
- Period of flowering during the year (month of start and end of flowering)
 - < 3 months = 0
 - Between 3 and 6 months = 1/2
 - >7 months = 1
- 4b. Very high seed output in favourable environmental circumstances
- Seed production per shoot (LEDA)
 - <381 = 0
 - 381-1031 = 1/3
 - 1031-5271 = 2/3
 - >5270 = 1
- 4c. Produces some seed in a wide range of environmental conditions; tolerant and plastic
- Ecotope amplitude (BioBase)
 - Wide (more than 2 ecotopes) = 1
 - Narrow = 0
- 4d. Has adaptations for long-distance dispersal (Standard list, Tamis *et al.* 2003)
- No adaptations to long-distance dispersal = 0
 - Adapted to dispersal by wind, water, mammals, birds or humans = 1/2
 - Adapted to two or more of these dispersal vectors = 1
- 4e. Seed size
- Seed size (Zaadatlas)
 - <1 mm = 1
 - 1-2 mm = 2/3
 - 2-3 mm = 1/3
 - >3 mm = 0

5. Dispersal by vegetative means

- 5a. Has vegetative reproduction (CLO-PLA)
- Plant fragments of stem origin that can root, long rhizomes, bulb or horizontal above ground stem = 1
 - Roots with adventitious buds = 3/4
 - Short rhizomes = 1/2
 - Root splitter (little spread) = 1/4
 - None = 0
- 5b. Can regenerate from fragments, i.e. regrowth capacity (BioBase)
- Phanerophyte = 0
 - Woody chamaephyte = 1/3
 - Herbaceous chamaephyte = 1/3
 - Hemicryptophyte = 2/3
 - Geophyte = 1
 - Therophyte = 0

6. Biotic interactions

- 6a. Has ability to compete interspecifically by special means
- 6a1. - Canopy height (BioBase)
- <5 cm = 0
 - 5-10 cm = 1/5
 - 10-30 cm = 2/5
 - 30-60 cm = 3/5
 - 60-100 cm = 4/5
 - >100 cm = 1
- 6a2.- Lateral spread in metres per year (CLO-PLA)
- <0.01 m/yr = 0.00
 - 0.01-0.25 m/yr = 1/2
 - >0.25 m/yr = 1
- 6b. Parasitic
- No parasite = 1
 - Hemiparasite = 1/2
 - Parasite = 0

8 Results

The 17 characters on the Baker+ list were compared for a subset of 10 of Keeler (1989)'s World's Worst Weeds which occur in the Netherlands¹, 16 Dutch worst weeds², a random selection of plant species from the Dutch flora, subdivided into ruderals, agrestals and other wild plants, and crops³.

The data for these six groups were compared using a non-parametric test (Kruskal-Wallis). For 11 of the 17 characters significant differences existed between the groups (denoted by * in Table 3). After applying Bonferoni-correction (Haccou & Meelis, 1992) 7 of the 17 characters are still significant (indicated by ** in Table 3).

Table 3: Average score¹ and standard error of weediness characteristics (Baker+ list) of the World's Worst Weeds (www), Dutch Worst Weeds (dww), random plants from the Dutch flora (ruderals (rud), agrestals (agr) and other wild species (woth)) and selected crop species (crop).

Baker + trait	www (n=10)	dww (n=16)	rud (n=52)	agr (n=69)	woth (n=40)	crop (n=24)
Germination time 1a1	0.10(0.10)	0.19(0.10)	0.17(0.05)	0.25(0.05)	0.18(0.06)	0.33(0.10)
Germination requirement 1a2*	0.90(0.07)	0.63(0.12)	0.75(0.06)	0.86(0.04)	0.83(0.06)	1.00(0)
Seedbank1b**	0.90(0.07)	0.83(0.07)	0.66(0.04)	0.83(0.03)	0.57(0.04)	0.54(0.06)
SLA 2a	0.58(0.08)	0.52(0.08)	0.51(0.04)	0.53(0.03)	0.45(0.05)	0.48(0.05)
Vegetative period 2b*	0.66(0.07)	0.69(0.07)	0.47(0.04)	0.58(0.03)	0.51(0.05)	0.48(0.05)
Pollination 3a,b*	0.60(0.07)	0.91(0.05)	0.86(0.03)	0.81(0.03)	0.79(0.04)	0.77(0.05)
Sex type 3c	1(0)	0.88(0.09)	0.98(0.02)	0.97(0.02)	1(0)	0.92(0.06)
Seed period. 4a**	0.50(0.07)	0.72(0.09)	0.49(0.03)	0.52(0.03)	0.49(0.05)	0.31(0.03)
Seed production 4b	0.60(0.12)	0.65(0.09)	0.53(0.05)	0.45(0.04)	0.47(0.06)	0.47(0.08)
Ecol. amplitude 4c**	-	0.19(0.10)	0.44(0.07)	0.12(0.04)	0.20(0.06)	0.25(0.09)
Dispersal 4d	0.60(0.10)	0.66(0.08)	0.54(0.05)	0.44(0.04)	0.55(0.06)	0.48(0.07)
Seed length 4e**	0.50(0.09)	0.60(0.07)	0.31(0.04)	0.56(0.04)	0.45(0.06)	0.14(0.05)
Veg. reproduction 5a**	0.50(0.12)	0.41(0.09)	0.61(0.06)	0.38(0.05)	0.65(0.06)	0.44(0.08)
Regrowth 5b*	0.33(0.14)	0.25(0.10)	0.55(0.05)	0.18(0.04)	0.55(0.05)	0.36(0.09)
Canopy height 6a1**	0.66(0.06)	0.55(0.04)	0.84(0.02)	0.55(0.02)	0.62(0.03)	0.83(0.03)
Lateral spread 6a2*	0.35(0.15)	0.22(0.08)	0.43(0.05)	0.18(0.03)	0.26(0.05)	0.27(0.06)
Parasite 6b	1(0)	1(0)	0.92(0.04)	0.98(0.02)	1(0)	1(0)
Sum score*	9.78(0.55)	9.86(0.47)	10.05(0.35)	9.18(0.34)	9.54(0.37)	9.07 (0.28)

¹ The higher the value, the more weedy the species.

* Denotes significant differences at $\alpha=0.05$ between groups based on Kruskal-Wallis test (traits) or ANOVA (sum score).

** Denotes significance after Bonferoni correction of trait analysis.

¹ *Amaranthus hybridus* (smooth amaranth)*, *Amaranthus spinosus* (spiny amaranth), *Avena fatua* (common wild oat)*, *Chenopodium album* (lamb's quarters)*, *Convolvulus arvensis* (field bindweed)*, *Cynodon dactylon* (couch grass)*, *Cyperus esculentus* (chufa sedge)*, *Cyperus rotundus* (nutgrass), *Digitaria sanguinalis* (hairy crabgrass)*, *Echinochloa colona* (jungle rice), *Echinochloa crus-galli* (cockspur)*, *Eleusine indica* (goose grass), *Imperata cylindrica* (blady grass), *Paspalum conjugatum* (hilograss), *Portulaca oleracea* (common purslane)*, *Rottboellia exaltata* (itchgrass), *Sorghum halepense* (Johnson grass)*. Species marked with a * are species occurring in the Netherlands. Because only information on these ten species was available in the databases, these were analyzed as our World's Worst Weeds.

² Chosen as the 20 Dutch worst weeds by our advisory committee were: *Alopecurus myosuroides* (black-grass), *Capsella bursa-pastoris* (shepherd's purse), *Chenopodium album*†, *Cirsium arvense* (creeping thistle), *Convolvulus arvensis*†, *Cyperus esculentus*†, *Diplotaxis tenuifolia* (perennial wall rocket), *Echinochloa crus-galli*†, *Equisetum arvense* (field horsetail), *Galinsoga parviflora* (gallant soldier), *Matricaria chamomilla* (German chamomile), *Poa annua* (annual meadow grass), *Polygonum persicaria* (redshank), *Polygonum aviculare* (common knotgrass), *Rorippa sylvestris* (creeping yellowcress), *Senecio vulgaris* (common groundsel), *Solanum nigrum* (black nightshade), *Stellaria media* (common chickweed), *Rumex acetosa* (sorrel) and *Teesdalia nudicaulis* (barestem teesdalia). Four of them, marked with a †, are also on the list of the World's Worst Weeds and are included only in that list to prevent double counting.

³ The selected crops included: *Apium graveolens* (celery), *Asparagus officinalis* (asparagus), *Brassica napus* (oilseed rape), *Cichorium endivia* (andive), *Cucumis sativus* (cucumber), *Foeniculum vulgare* (fennel), *Fragaria X ananassa* (strawberry), *Lactuca sativa* (lettuce), *Phaseolus vulgaris* (common bean), *Pisum sativum* (pea), *Rheum rhabarbarum* (rhubarb), *Scorzonera hispanica* (black salsify), *Spinacia oleracea* (spinach), *Vicia faba* (broad bean), *Avena sativa* (oats), *Hordeum vulgare* (barley), *Medicago sativa* (alfalfa), *Secale cereale* (rye), *Solanum tuberosum* (potato), *Triticum aestivum* (wheat), *Triticale X Triticosecale* (hybrid wheat and rye) and *Zea mays* (corn).

The Kruskal-Wallis test indicates which groups are different. Most relevant for our purpose is the contrast between weeds, plants from the Dutch flora and crops. Crops typically had a short period of flowering and seed production (trait 4b in the Baker+ list) as compared with plants from the Dutch flora and with weeds (Fig.4A). Crops also have relatively big seeds (trait 4e) as compared with all other groups (Fig.4B). When comparing the weeds with the other groups, it is apparent that the weeds more often have a persistent seed bank in the soil (trait 1b, Fig.4D) and have a short vegetative period before first flowering (trait 2b, Fig.4C), although this latter result is no longer significant after Bonferroni correction. The characters canopy height (6a1), ecological amplitude (4c) and vegetative reproduction (5a) are also significantly different between groups after Bonferroni correction. Crops are apparently tall, which should positively effect their competitive ability and hence their weediness. Crops score intermediate with respect to ecological amplitude. Since ecological amplitude for crop species is not in the databases but was entered by us subjectively, the latter conclusion has limited value. Vegetative reproduction is typically low for plants that grow on the field (crops, agrestals, weeds) as compared with ruderals and other wild plants.

As expected, the total score, i.e. the sum of the 17 characters from the Baker+ list, was lowest for crops. However, the differences from the other groups were quite small and, surprisingly, weeds did not score higher than random plants from the Dutch flora. The plant species with the highest scores were *Artemisia vulgaris* (13.7), *Urtica dioica* (13.3), *Rumex crispus* (12.7) and *Rubus idaeus* (12.6). The lowest-scoring species were *Ranunculus acris* (6.1), *Pathenocissus inserta* (6.2) and *Cichorium endivia* (6.4).

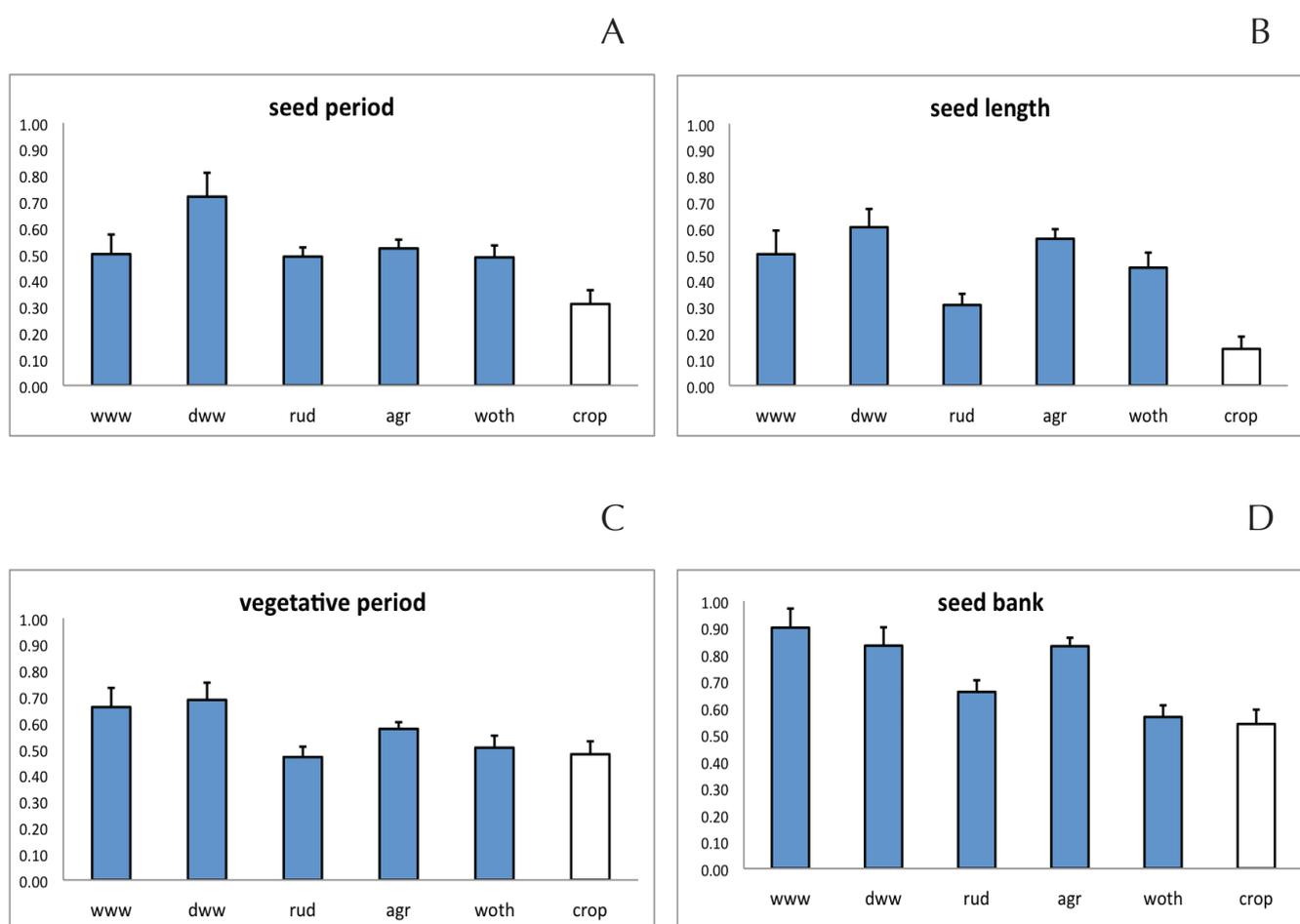


Fig.4 A-D: Comparison of major weediness characteristics between the World's Worst Weeds (www), Dutch Worst Weeds (dww), Dutch wild plants (ruderals (rud), agrestals (agr) and others (woth)) and crops (crop), indicating the mean and the standard error (SE). This is a selection of characteristics from Table 1 that highlights the main differences between crops, wild plants and weeds. The Y-axis gives the degree of weediness as scored in Table 3. High values for weediness are associated with a long period of flowering and seed production, small seed length, a short vegetative period before flowering and the existence of a long-lived seed bank.

Interesting differences in weedy characters emerge. Crops have relatively large seeds and a short period of flowering and seed production, but otherwise there are few differences between crops and plants from the wild flora. Weeds more often have a persistent seed bank in the soil and have a shorter vegetative period; they start flowering earlier in life. Significant as these data may be, there is considerable overlap between groups and this makes it difficult to predict for any given crop species whether it could form populations outside the agricultural field or even become a troublesome weed. Summation of the scores for all 17 characters from the Baker+ list did not lead to clear-cut differences between groups, as was suggested by Keeler (1989). With our method of quantification and using existing databases we cannot reproduce her results. This raises the question how Keeler's results compare with ours when we consider the same group of species. The characters used by Keeler (1989) largely overlap with the set we used. We did not use brittleness, "reported as weed" and polyploidy from her list, but instead added seed size, sex type, regrowth capacity and parasitic/non-parasitic. Sex system is not informative because few species are dioecious. Similarly, there are hardly any parasitic plants in our sample. Regrowth capacity differs significantly between groups; this character is much lower in agrestals than in other wild plants but does little to distinguish the other groups. Seed size is a valuable addition to the Baker scheme since it clearly distinguishes the crops (large seeds) from the wild plants and weeds (small seeds). The small differences in the characters chosen between our study and that of Keeler (1989) do not explain the difference between her results and ours (Table 4). The scores from the wild plants from the UK and the Netherlands are very similar and for this group Keeler (1989) consulted the Biological Flora of the British Isles, which contains accurate data on the species covered. We evaluate the World's Worst Weeds differently from Keeler. This is not due to a sampling error. We selected 10 species from the 17 world's worst weeds from Keeler (1989) because this subset grows in the Netherlands and life-history data are readily available. Comparing the 10 selected weeds with the 7 we did not select with respect to their score in Keeler's (1989) Table 1 showed no differences in the number of weediness traits. Thus the scoring of weedy characters in the world's worst weeds by Keeler is systematically higher than in our scoring. The scoring of weedy characters of crops by Keeler (1989) is lower than with our method. In this case, however, the difference is less pronounced and different crop species were selected in the different studies.

Table 4. Comparison of the average percentage of the maximum score in the dataset of Keeler (1989) and our dataset; a plant species attains the maximum score of 100% if it scores 1 on all 16 (Keeler 1989) or 17 points (our method).

	Keeler (1989)	Our data
World's Worst Weeds	85.6%	57.5%
Dutch Worst Weeds	-	58.0%
Flora of Britain	59.0%	-
Dutch flora	-	58.9%
Crops	42.0%	53.9%

The summation of weediness traits was used in previous studies (Keeler 1989) and therefore we used this as a starting point. One could argue that some characters are more important than others and should be valued accordingly. Also, in the summation some characters for which the crops score high apparently obscure the 4 important differences in which crops differ from wild plants and weeds. A weighting of characters or using them in a multiplicative way might therefore improve separation between the groups. For instance, if we multiply the four characters in Fig.4, 19 out of 24 crops score zero, i.e. they score lowest on the weediness scale for at least one character. For the remaining plants only 66 out of 187 species score zero. This difference is highly significant ($P=4.5 \cdot 10^{-5}$ in a Chi-square test) but not black and white, as there are some wild plants that also score zero and a few crop plants that score higher than zero.

Cross tabulation with respect to seed size and the period of flowering and seed production shows better separation between crops, wild plants and all weeds (Dutch weeds plus World's Worst Weeds) (Table 5) than summation. Crops are concentrated in the top left-hand corner of the matrix of Table 5 (low scores for both weedy characters), wild plants in the centre and weeds are in the bottom right hand corner, with a high score for both characters. This method gives a clearer separation than summation of all 17 scores for weediness. Nevertheless, there remains an overlap. It is quite possible that more elaborate statistical methods like multivariate techniques (for instance, Redundancy Analysis or Discriminant Analysis) would allow clearer separation of the groups. Although we are currently engaged in such analyses, these are beyond the time frame available for this report.

Table 5: Number of species tabulated for weediness based on seed size in 5 classes (0, 0.33, 0.50, 0.67 and 1 with low seed size giving the highest score) in the horizontal direction and weediness based on flowering period (0, 0.5, 1 with long continued flowering and seed set giving the highest score) in the vertical direction.

Crops	0	0.33	0.50	0.67	1
0	8	2	0	0	0
0.5	8	2	0	3	0
1	1	0	0	0	0

Wild plants	0	0.33	0.50	0.67	1
0	10	4	0	5	4
0.5	29	21	6	42	16
1	5	8	0	11	0

All weeds	0	0.33	0.50	0.67	1
0	0	0	0	2	1
0.5	2	2	0	7	2
1	1	3	0	6	0

9 Assessment of selected crop species

Using the Baker+ list in standardized fashion, we collected the weedy characters for three selected crop species, viz. oilseed rape (*Brassica napus*), potato (*Solanum tuberosum*) and apple (*Malus sylvestris*). We also sent a questionnaire (see Appendix 2) to the following experts: Dr. Peter Bruinenberg (Avebe, potato), Dr. Elze Hesse (Leiden University, oilseed rape) and Dr. Henk Schouten (PRI, Wageningen University, apple). Their answers were generally consistent with the information in the databases. An exception is that potato seeds can apparently survive in the soil for over 4 years, so that potato should probably score higher on this character than the databases indicate. Potatoes can make up to 10 fruits per plant with up to 200 seeds per fruit. This also gives a higher score for point 4b than the databases. It can be questioned how well apples are dispersed. Birds do not easily disperse apples, so this would hamper long-distance dispersal. On the other hand, humans aid dispersal when they dispense of apple cores. Seeds of oilseed rape are 2-2.5 mm and should score 0.33 rather than the 0.67 indicated in the Zaadatlas. There is apparently some inaccuracy in the databases.

Potato

The total weediness score of potato in Table 6 is close to the average of wild plants in Table 3. We concluded that big seeds and a short period of flowering were crop characters. Potato scores 0.33 for seed size, showing that seeds are not very large (2-3mm) and the plant has a short period of flowering and seed production (score 0). A long-lived seed bank and a short vegetative period before flowering are weed characters. Potato seeds can survive in the soil for over 4 years. Potato scores intermediate with respect to vegetative period before flowering. There is little in this analysis that leads to the common knowledge that potato is not a weed and does not establish feral self-supporting populations. Why, then, does potato not exhibit such behaviour and what genetic modifications might make it feral?

Dr. Bruinenberg pointed out that the original wild stock of *S. tuberosum* from South America was diploid with $2n=24$ while cultivated potatoes are tetraploid. Thus the potatoes as we grow them do not occur in the wild. Poor winter survival of tubers has often been cited as a critical factor for potato establishment, as frost kills tubers after only a few days. However, a recent COGEM report by van de Wiel *et al.* (2011) pointed out that critical temperatures of below -2°C occur rarely, 7 times in 30 years, at 10 cm soil depth in the Netherlands. In most years tubers survive and the species could overwinter under extreme conditions as a seed. In conclusion, it is evident from past agricultural experience that potato does not 'go wild', but the reasons for this are unclear. Demographic studies comparing different varieties could show how frequently seedlings establish and where the life cycle of the plant stalls.

Oilseed rape

The total weediness score of oilseed rape is also average and close to that of potato (Table 6). Oilseed rape scores 0.67 for seed size, due to its relatively large seeds. The flowering period is intermediate (score 0.5), individual plants can extend their flowering for a few weeks under favourable conditions, but eventually the many developing seeds claim all resources and flowering stops. Because of differences in time of germination, flowering plants can be found later in the year, too. *B. napus* can best be compared with its close relative *B. rapa*, which is a common wild plant in the west of the Netherlands (Luijten & de Jong 2011). *B. napus* populations are typically small, are found under very disturbed conditions and are associated with seed spillage during transport (Luijten & de Jong 2011). There are probably no self-supporting populations of *B. napus* in the Netherlands and the species is certainly not invasive. Dr. Hesse (Leiden University) carried out demographic studies with financial support from the ERGO/NWO programme, establishing experimental populations (9 wild *B. rapa* accessions, 10 *B. napus* accessions sampled in the wild, 10 *B. rapa* crops, including both recent and old ones) at two locations in the Netherlands. While after sowing the seeds on empty soil in August all populations established well and flowered abundantly the next spring, she found that in the subsequent year populations of *B. rapa* and of ancient cultivars of *B. napus* persisted, while all other modern varieties of *B. napus* had already disappeared. She measured seed survival after burial and found that while most *B. rapa* seeds survive a year in the soil, *B. napus* seeds have poor survival. *B. rapa* seeds are smaller and have a much thicker seed coat. Dr Hesse emphasized that the surviving lines all germinated throughout the season, while the other *B. napus* accessions and modern cultivars typically germinated in autumn, directly after seed dispersal. She emphasized the stronger competitive ability of established plants of *B. rapa* as compared with *B. napus*. The modern cultivars of *B. napus* all had low glucosinolate content. Glucosinolates were higher in ancient *B. napus* crops and highest in the wild *B. rapa* plants. The consequences of glucosinolate content for leaf and seed herbivory are currently being researched, but the working hypothesis is that high glucosinolate content reduces both leaf herbivory and seed predation. All data have been collected and will be analyzed in 2012. If these results are related to the Baker+ list, we can say that oilseed rape

differs from its wild relative *B. rapa* by having lost the ability to germinate in autumn and spring (character 1a in the Baker+ list), while most cultivars form no seedbank (1b) and *B. napus* has larger seeds (4e) and is less competitive (6). All changes are in the direction of less weediness according to the Baker+ list. In addition, domestication of oilseed rape has resulted in a decrease of secondary plant substances that probably renders the plant more resistant to herbivory and reduces seed production (4b).

Apple

Apple scores very low on many aspects of weediness but this result is of limited value since the characters we listed were not meant for woody plants or plants in situations other than pioneer habitats. Apple trees are an unlikely weed, but may still occur in later successional stages with shrubs and trees. A restriction of our study is that we focused on arable fields and highly disturbed adjacent habitats. Dr. Schouten stated that wild apple trees growing in the Netherlands are typically due to people throwing away apple cores. Cultivated apples suffer from a number of diseases including scab (*Venturia inaequalis*), mildew (*Podosphaera leucotricha*), cancer (*Nectra galligena*), aphids and bacteria (e.g. *Erwinia amylovora*) and galls (*Agrobacterium tumefaciens*). While wild relatives have some resistance, they too are often also susceptible to these diseases. Truly wild apples disappeared from the Netherlands because they produced insufficient viable offspring.

Table 6: Score on the Baker+ list for selected crop species (oilseed rape, potato, apple), according to the databases and experts (the latter in brackets).

Baker trait	<i>B. napus</i>	<i>S. tuberosum</i>	<i>M. sylvestris</i>
Germination time 1a1	0	0	0
Germination requirement 1a2	1	1	0
Seedbank1b	0.67	0.33 (or 1)	0
SLA 2a	0.5	0.67	0
Vegetative period 2b	0.4	0.6	0
Pollination 3a,b	1	1	0.5
Sex type 3c	1	1	1
Seed period 4a	0.5	0	0
Seed production 4b	1	0 (or 0.67)	1
Ecol. amplitude 4c	0	0	0
Dispersal 4d	0	0.5	1
Seed length 4e	0.67 (or 0.33)	0.33	0
Veg. reproduction 5a	0	1	0
Regrowth 5b	0.67	1	0
Canopy height 6a1	0.8	0.8	1
Lateral spread 6a2	0.5	0.5	0
Parasite 6b	1	1	1
<i>Total</i>	9.71 (10.04)	9.73 (11.07)	5.5

10 Discussion and recommendations

Our analysis showed that crops have significantly bigger seeds and a shorter period of flowering and seed production than wild plants. A long period of flowering and seed production also emerged as a weedy character from the analysis of Perrins *et al.* (1992a) and Speek *et al.* (2011). Compared with weeds, crops also differ in lacking a long-lived seed bank in the soil and having a long vegetative period. All these differences are in the direction predicted by Baker and subsequent authors, and of potential use for pre-screening plants for weediness. Nevertheless, the differences between crops, wild plants and weeds are gradual and do not lead to the black and white picture we had imagined at the start of this project. It seems that Keeler's (1989) evaluation was partly on subjective grounds and cannot readily be reproduced or improved using the existing botanical databases. Our study demonstrated how data can be collected in an objective manner.

Our analysis still leaves room for improvement. One issue not addressed by Baker (1965) or ourselves is herbivory, for example. Negative effects of herbivory on individual plants have been well quantified and one can well imagine that plant species that are consumed less by herbivores become more common or are more weedy than species that are not eaten by herbivores. Maron & Crone (2006) have evaluated the effects of herbivory on species abundance, and emphasize that we know relatively little. One could relate herbivore pressure to foliar damage, but this is just one aspect of herbivory. Vasquez and Meyer (2011) found that spraying with insecticide greatly improved the performance of *Pastinaca sativa*, while this species showed low levels of foliar damage. Apparently the plant suffers from herbivores that are less visible. Herbivory can affect seed production and in this way reduce recruitment, especially in open and half-open habitats. Maron & Crone (2006) give several examples that support this scenario.

It is conceivable that plant species that are released from their herbivores increase in abundance. In relation to invasive plants, especially those that enter an entirely new habitat in which their specialist herbivores are absent, this idea is known as the 'enemy release hypothesis'. Behind this hypothesis is the idea that herbivores regulate plant populations. Additionally, it is assumed that herbivores affect invasive aliens less than native species. While this may well be the case, the point should be checked rather than being taken for granted. Roy *et al.* (2011) have concluded that empirical evidence for the role of herbivory in invasion success was lacking. Protection against certain herbivores, for instance by a transgene, may thus increase weediness in some cases but not always. Measuring herbivory and including it as a component of weediness certainly seems a worthwhile extension of the Baker list.

Where does this leave us with respect to predicting whether or not a crop can potentially produce volunteers and escape from the agricultural field into disturbed habitats? The four key characters identified (seed size, flowering period, seed bank, vegetative period) can be used for initial screening. These characters and others on the Baker+ list also provide a reference point when evaluating the weediness of crops, their wild relatives and their transgenic varieties. Our analysis was based on general life-history characteristics that were independent of climate or geography. Additional information from the WRA list could also be used. Perennial plants that cannot withstand Dutch winters cannot grow here, and a climate match will increase the likelihood of a plant becoming a weed. If a plant species or a closest relative is already a weed in other parts of its geographical range, the probability is higher that it will become a weed here. In addition, highly domesticated species are less likely to become weeds.

Our Baker+ list could also provide a starting point for quantifying how far cultivars are removed from their wild ancestor with respect to weediness characters. Similarly a list can be made of GM-characters that, according to the Baker list, affect weediness in a negative or positive way.

For the COGEM the question whether insertion of one or more transgenes could transform a crop from tame to weedy or wild is of utmost importance. This question can be answered when you know the key life-stages that limit population growth in a specific species. Our study only gives some general guidelines about which traits are most likely to increase weediness. GM traits that decrease seed size, lengthen the period of flowering and seed production, lead to more persistent seed banks and a short vegetative phase, should be viewed with caution. Similarly traits for better seed dispersal or a higher growth rate (higher seed production) increase weediness according to Baker's list, although we could not confirm this idea. Many genetic modifications go in the opposite direction (for instance, less seed shattering) and lead to further domestication. Whether transgenes that decrease herbivory (for instance, Bt genes) would increase population growth is an interesting question for further research that we have not answered.

In conclusion, there are certain general guidelines based on plant life history that can be used to predict whether or not a crop can develop into a wild plant and a weed and these have been listed in this report. These guidelines may contribute to the pre-screening process. For specific situations, additional information can be derived from past

experience, geographical range and the history of cultivation of the species. Together these guidelines can lead to statements that it is unlikely or extremely unlikely that a given crop or crops will 'go wild'. In many cases, though, it will remain unclear what are the critical stages in the life cycle that prevent plant populations from growing. Detailed demographic studies can answer such questions, as exemplified by the research of Dr. Hesse on *Brassica napus* and *B. rapa*. Considering this scientific uncertainty, it is perhaps good to conclude with the empirical observation that most crops stay tame and very few crops have become weeds (Warwick & Stewart 2005). Scientific uncertainty is not the same as perceived risk. Or to put it another way, although we are currently ignorant of the causal factors that keep potato tame in the Netherlands, this does not alter the fact that potatoes are (almost) never found growing wild here.

Acknowledgements

We thank Peter Bruinenberg, Henk Schouten and Elze Hesse for filling in the questionnaire and Nigel Harle for brushing up our English.

References

- Adams C.D. & Baker H.G. (1962) "Weeds of cultivation and grazing lands". In: *"Agriculture and land use in Ghana"* edited by J. B. Wills, pp. 402-415. Oxford University Press, London.
- Allard R.W. (1965) "Genetic systems associated with colonizing ability in predominantly self-pollinated species." In: *"The genetics of colonizing species"*, edited by H.G. Baker & G.L. Stebbins, pp. 50-76. Academic Press, NY.
- Aptekar R. & Rejmánek M. (2000) "The effect of seawater submergence on rhizome bud viability of introduced and native dune grasses (*Ammophila arenaria* and *Leymus mollis*) in California." *J. Coast. Conserv.* 6: 107-111.
- Auld B.A., Hosking J. & McFadyen R.E. (1983) "Analysis of the spread of tiger pear and parthenium weed in Australia." *Aust. Weeds* 2: 56-60.
- Baker H.G. (1953) "Race formation and reproductive method in flowering plants." *Symp. Soc. Exp. Biol.* 7: 114-45.
- Baker H.G. (1954) "Report of paper presented to meeting of British Ecological Society." *J. Ecol.* 42: 571.
- Baker H.G. (1955). "Self-compatibility and establishment after "long-distance" dispersal." *Evolution* 9: 347-348.
- Baker H.G. (1962) "Weeds - native and introduced." *J. Calif. Hort. Soc.* 23: 97-104.
- Baker H.G. (1965) "Characteristics and modes of origin of weeds." In: *"The genetics of colonizing species"*, edited by H.G. Baker & G.L. Stebbins, pp. 147-172. Academic Press, NY.
- Baker H.G. (1967) "The evolution of weedy taxa in the *Eupatorium microstemon* species aggregate." *Taxon* 16:293-300.
- Baker H.G. (1972) "Human influences on plant evolution." *Econ. Bot.* 26: 32-43
- Baker H.G. (1972) "Seed weight in relation to environmental conditions in California." *Ecology* 53: 997-1010.
- Baker H.G. (1974) "The evolution of weeds" *Ann. Rev. Ecol. Syst.* 5: 1-24.
- Baskin C.C. & Baskin J.M. (2003) *"Seeds: ecology, biogeography and evolution of dormancy and germination."* Academic Press, San Diego.
- Basu C. et al. (2004) "Weed genomics: new tools to understand weed biology." *Trends Plant Sc.* 9: 391-398.
- Bennett M.D., Leitch I. J. & Hanson L. (1998) "DNA amounts in two samples of angiosperm weeds." *Ann. Bot.* 82(Suppl.A): 121-134.
- Binggeli P. (1996) "A taxonomic, biogeographical and ecological overview of invasive woody plants." *J. Veg. Sci.* 7: 121-124.
- Booth B.D., Murphy S.D. & Swanton C.J. (2003) *"Weed ecology in natural and agricultural systems"* CABI Publishing, Oxfordshire.
- Boyce M.S. (1984) "Restitution of *r*- and *K*-selection as a model of density-dependent natural selection." *Annu. Rev. Ecol. Syst.* 15: 427-447.
- Chancellor A.P. (1968) "The value of biological studies in weed control" *Proc. 9th Brit. Weed Contr. Conf.*, 1129-1135.
- Crawley M.J., Harvey P. H. & Purvis A. (1996) "Comparative ecology of the native and alien floras of the British Isles". *Phil. Trans. R. Soc. Lond. B* 351: 1251-1259.
- Cumming B.G. (1959) "Extreme sensitivity at germination and photoperiodic reaction in the genus *Chenopodium* (Tourn.) L." *Nature* 184: 1044-1045.
- Daehler C.C. (2003) "Performance comparisons of co-occurring native and alien plants: Implications for conservation and restoration." *Annu. Rev. Ecol. Evol. Syst.* 34:183-211.
- Darwin C. (1859) *"The origin of species by means of natural selection."* Murray, London.
- EFSA Panel on Genetically Modified Organisms (2010) "Guidance on the environmental risk assessment of genetically modified plants." *EFSA Journal* 8(11): 1879 (111pp.).
- Egler F. E. (1983) "The nature of naturalization II. The introduced flora of Aton Forest, Connecticut." Claude E. Phillips Herbarium Publication no. 6. Delaware State College, Dover.
- Forcella F. & Wood J. T. (1984) "Colonization potentials of alien weeds are related to their 'native' distributions: implications for plant quarantine." *J. Aust. Inst. Agr. Sci.* 50: 36-40.
- Fryxell P. (1957) "Mode of reproduction of higher plants." *Bot. Rev.* 23: 125-233.

- Gaudet C.L. & Keddy P.A. (1988) "A comparative approach to predicting competitive ability from plant traits." *Nature* 334: 242–243.
- Goodin B.J., McAllister A.J. & Fahrig L. (1998) "Predicting invasiveness of plant species based on biological information." *Conserv. Biol.* 13: 422–426.
- Gordon, D.R. *et al.* (2008) "Consistent accuracy of the Australian weed risk assessment system across varied geographies." *Diversity and Distributions* 14: 234-242.
- Grime J.P, Hodgson, J.G & Hunt, R. (1988, 2nd edition 2007) "*Comparative plant ecology*", Castlepoint Press.
- Grime J.P. & Hunt R. (1975). "Relative Growth-Rate: its range and adaptive significance in a local flora." *J. Ecol.* 63: 393-422.
- Grime, J.P. (1979) "*Plant strategies and vegetation processes*." John Wiley, New York.
- Grotkopp E., Stoltenberg R., Rejmánek M. & Rost T. (1998) "The effect of genome size on invasiveness." *Amer. J. Bot.* 85 Suppl.: 34.
- Haccou P. & Meelis E. (1992) "*Statistical analysis of behavioural data; an approach based on time-structured models*", Oxford University Press, Oxford.
- Hancock J.F. (2003) "A framework for assessing the risk of transgenic crops." *BioScience* 53: 512-519.
- Harper J.L. (1977) "*Population biology of plants*", Academic Press, New York
- Hayes K.R. & Barry S.C. (2008) "Are there any consistent predictors of invasion success?" *Biol. Invasions* 10: 483-506.
- Henderson L. (1991) "Alien invasive *Salix* spp. (willows) in the grassland biome of South Africa." *S. Afr. For. J.* 157: 91–95.
- Henslow G. (1891) "*The making of flowers*." Soc. Propagation Christian Knowledge, London.
- Hodgson J.G., Wilson P.J., Hunt R., Grime J.P. & Thompson K. (1999) "Allocating C-S-R plant functional types: a soft approach to a hard problem." *Oikos* 85: 252-294.
- Hodkinson D.J. & Thompson K. (1997) Plant dispersal: the role of man. *J. Appl. Ecol.* 34: 1484–1496.
- Holm R.E. & Miller M.R. (1972) "Hormonal control of weed seed germination." *Weed Sci.* 20: 209-12.
- Keeler K.H. (1989) "Can genetically engineered crops become weeds?" *Biotechnology* 7: 1134-1139.
- King L.J. (1966) "*Weeds of the world: biology and control*." L. Hill, London.
- Lewontin R.C. (1965) "Selection for colonizing ability" In: "*The genetics of colonizing species*" edited by H.G. Baker & G.L. Stebbins, pp. 77-91. Academic Press, New York.
- Luijten S.H. & de Jong T.J. (2010) "A baseline study of the distribution and morphology of *Brassica napus* L. and *Brassica rapa* L. in the Netherlands." COGEM Report 2010-3.
- MacArthur R.H. & Wilson E.O. (1967) "*The theory of island biogeography*.", Princeton University Press, Princeton.
- Malíková L., Šmilauer P. & Klimešová, J. (2010) "Occurrence of adventitious sprouting in short-lived monocarpic herbs: a field study of 22 weedy species." *Ann. Bot.* 105: 905–912.
- Maron J.L. & Crone E. (2006) "Herbivory: effects on plant abundance, distribution and population growth." *Proc. Royal Soc. B* 273: 2575-2584.
- Milla R., Reich P. B., Niinemets U. & Castro-Diez P. (2008) "Environmental and developmental controls on specific leaf area are little modified by leaf allometry." *Funct. Ecol.* 22: 565-576.
- Müller-Dombois D. & Ellenberg H. (1974) "*Aims and methods in vegetation ecology*." John Wiley, New York.
- Mulligan G.A. & Findlay, J.N. (1970) "Reproductive systems and colonization in Canadian weeds." *Can. J. Bot.* 48: 859-60.
- Mulligan, G.A. (1972) "Autogamy, allogamy and pollination in some Canadian weeds." *Can. J. Bot.* 50: 1767-1771.
- Pandit M.K., Pockock M.J.O. & Kunin W.E. (2011) "Ploidy influences rarity and invasiveness in plants" *J. Ecol.* 99: 1108-1115.
- Panetta F.D. & Scanlan J.C. (1995) "Human involvement in the spread of noxious weeds: what plants should be declared and when should control be enforced?" *Pl. Prot. Quart.* 10: 69–74.
- Perrins J. *et al.* (1992a) "A survey of differing views of weed classification: implications for regulation of introductions." *Biol. Cons.* 60: 47-56.

- Perrins J., Williamson M. & Fitter A. (1992b) "Do annual weeds have predictable characters?" *Acta Oecol.* 13: 517-533.
- Pheloung P. *et al.* (1999) "A weed risk assessment model for use as a biosecurity tool evaluating plant introductions." *J. Environ. Manage.* 57: 239-251.
- Pieterse A.H. & Murphy K.J. (1990) "*Aquatic Weeds.*" Oxford University Press, Oxford.
- Poorter H. & van der Werf A. (1998) "Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species." In: "*Inherent variation in plant growth. Physiological mechanisms and ecological consequences*", edited by Lambers H., Poorter H. & van Vuuren M.M.I., pp. 309-336. Backhuys Publishers, Leiden.
- Pysek P., Prach K. & Smilauer P. (1995) "Relating invasion success to plant traits: an analysis of the Czech alien flora." In: "*Plant invasions*" edited by P. Pysek, K. Prach, M. Rejmánek & Wade P. M., pp. 237-247. SPB Academic Publishing, The Hague.
- Pysek P. *et al.* (2004a) "Alien plants in checklists and floras: towards better communication between taxonomists and ecologists." *Taxon* 53: 131-143.
- Pysek P. *et al.* (2004b) "Predicting and explaining plant invasions through analysis of source area floras: some critical considerations." *Diversity and Distributions* 10: 179-187.
- Rejmánek M. (1995) "What makes a species invasive?" In: "*Plant invasions*" edited by P. Pysek, K. Prach, M. Rejmánek & P. M. Wade, pp. 3-13. SPB Academic Publishing, The Hague.
- Rejmánek M. (1996a) "A theory of seed plant invasiveness: the first sketch." *Biol. Conserv.* 78, 171-181.
- Rejmánek M. (1996b) "Species richness and resistance to invasions." In: "*Diversity and processes in tropical forest ecosystems*" edited by G. H. Orians, R. Dirzo & J. H. Cushman, pp. 153-72. Springer Verlag, Berlin.
- Rejmánek M. & Richardson D.M. (1996) "What attributes make some plant species more invasive?" *Ecology* 77: 1655-1661.
- Rejmánek M. (1999) "Invasive plant species and invulnerable ecosystems." In: "*Invasive species and biodiversity management*" edited by O. T. Sandlund, P. J. Schei & A. Vilken, pp. 79-102. Kluwer, Dordrecht.
- Rejmánek M. (2000) "Invasive plants: approaches and predictions." *Aust. Ecol.* 25: 497-506.
- Richardson D.M. *et al.* (2000) "Plant invasions - the role of mutualisms." *Biol. Rev.* 75: 65-93.
- Roy H.E. *et al.* (2011) Can the enemy release hypothesis explain the success of invasive alien predators and parasitoids? *Biocontrol* 56: 451-468.
- Salisbury E.J. (1961) "*Weeds and aliens*". Collins, London.
- Schaefer H. *et al.* (2011) "Testing Darwin's naturalization hypothesis in the Azores." *Ecol. Lett.* 14: 389-396.
- Schön I., Martens K. & van Dijk P. (2009) "*Lost sex: The evolutionary biology of parthenogenesis*". Springer, Berlin.
- Speek T.A.A. *et al.* (2011) "Factors relating to regional and local success of exotic plant species in their new range." *Diversity and Distributions* 17: 542-551.
- UCPE (1996) *Unit of Comparative Plant Ecology Annual Report*. University of Sheffield, Sheffield, UK.
- Vasquez E.C. & Meyer G.A. (2011) Relationships among leaf damage, natural enemy release, and abundance in exotic and native prairie plants. *Biol. Invasions* 13: 621-633.
- Warwick S. I. *et al.* (2009) "Gene flow, invasiveness, and ecological impact of genetically modified crops." *Ann. N.Y. Acad. Sc.* 1168: 72-99.
- Warwick S.I & Stewart Jr. C.N. (2005) "Crops come from wild plants – How domestication, transgenes, and linkage together shape fertility." In: "*Crop fertility and volunteerism*" edited by J. Gressel, pp. 9-30. CRC Press, Boca Raton.
- Wesson G. & Wareing P. F. (1969) "The role of light in the germination of naturally occurring populations of buried weed seeds" *J. Exp. Bot.* 20:402-13
- Wiel C.C.M van de *et al.* (2011). Crop volunteers and climate change. COGEM report 2011-11.
- Williamson M. (1993) "Invaders, weeds and the risk from genetically manipulated organisms." *Experientia* 49: 219-224.
- Williamson M. & Fitter A. (1996) "The characters of successful invaders." *Biol. Cons.* 78: 163-170.

Databases used

CBS (1997) "*BioBase*". Register biodiversiteit.

Cappers R.T.J., Bekker R.M. & Jans J.E.A. (2006) "*Digitale zadenatlas*". Groningen Archaeological Studies 4, Barkhuis Publishing, Groningen, Nederland. <http://seeds.eldoc.ub.rug.nl/>

Kleyer M. *et al.* (2008): The LEDA traitbase: a database of life-history traits of Northwest European flora. *J. Ecol.* 96: 1266-1274. www.leda-traitbase.org

Klimešová J. & Klimes L. (2006) "*Clo-Pla3 – database of clonal growth of plants from Central Europe*". <http://clopla.butbn.cas.cz> **See also:** Klimešová J. & de Bello F. CLO-PLA: the database of clonal and bud bank traits of Central European flora. *J. Veget. Sc.* 20: 511-516.

Fitter A .H. & Peat H. J. (1994) The Ecological Flora Database. *J. Ecol.* 82, 415-425. <http://www.ecoflora.co.uk>

Tamis W.L.M. *et al.* (2003) "*Standaardlijst van de Nederlandse flora 2003*". <http://www.floron.nl>

Kew DNA Bank Database. <http://data.kew.org/dnabank/DnaBankForm.html>

Appendix 1. WRA Questionnaire

Domestication/ cultivation	1.01	Is the species highly domesticated?
	1.02	Has the species become naturalized where grown?
	1.03	Does the species have weedy races?
Climate and distribution	2.01	Species suited to (Australian) climates?
	2.02	Quality of climate match data
	2.03	Broad climate suitability (environmental versatility)
	2.04	Native or naturalized in regions with extended dry periods
	2.05	Does the species have a history of repeated introductions outside its natural range?
Weed elsewhere	3.01	Naturalized beyond native range
	3.02	Garden/amenity/disturbance weed
	3.03	Weed of agriculture/horticulture/forestry
	3.04	Environmental weed
	3.05	Congeneric weed
Undesirable traits	4.01	Produces spines, thorns or burrs
	4.02	Allelopathic
	4.03	Parasitic
	4.04	Unpalatable to grazing animals
	4.05	Toxic to animals
	4.06	Host for recognized pests and pathogens
	4.07	Causes allergies or is otherwise toxic to humans
	4.08	Creates a fire hazard in natural ecosystems
	4.09	Is a shade tolerant plant at some stage of its life cycle
	4.10	Grows on infertile soils
	4.11	Climbing or smothering growth habit
	4.12	Forms dense thickets
Plant type	5.01	Aquatic
	5.02	Grass
	5.03	Nitrogen fixing woody plant
	5.04	Geophyte
Reproduction	6.01	Substantial reproductive failure in native habitat
	6.02	Produces viable seed
	6.03	Hybridizes naturally
	6.04	Self-fertilization
	6.05	Requires specialist pollinators
	6.06	Reproduction by vegetative propagation
	6.07	Minimum generative time (years)
Dispersal mechanism	7.01	Propagules likely to be dispersed unintentionally
	7.02	Propagules dispersed intentionally by people
	7.03	Propagules likely to disperse as product contaminant
	7.04	Propagules adapted to wind dispersal
	7.05	Propagules buoyant
	7.06	Propagules bird dispersed
	7.07	Propagules dispersed by other animals (externally)
	7.08	Propagules dispersed by other animals (internally)
Persistence attributes	8.01	Prolific seed production
	8.02	Evidence that a persistent seed bank is formed (>1 year)
	8.03	Well controlled by herbicides
	8.04	Tolerates or benefits from mutilation, cultivation or fire
	8.05	Effective natural enemies present (in Australia)

Appendix 2. Dutch questionnaire on crops (apple, potato, oilseed rape)

Vragenlijst voor gewassen (appel/ aardappel/ koolzaad)

Algemeen

1. Wat is het ploïdie-niveau van dit gewas en wat is het chromosoomaantal?
2. Wat is de hoeveelheid DNA in pg per cel?
3. Is de soort (als deze buiten cultivatie zou groeien) eenjarig, tweejarig of overblijvend?
4. Wat is de "specific leaf area" (oppervlakte per gram blad) van deze soort onder niet beschaduwde omstandigheden?
5. Wat is de gemiddelde hoogte van de plant?
6. Kan de plant zich vegetatief reproduceren? Zo ja, op welke wijze (bijvoorbeeld met een horizontale bovengrondse stam of rhizomen)?
7. Hoeveel vegetatieve verspreiding heeft de plant zich in horizontale richting, minder dan 0.01 m/jaar, tussen 0.01 en 0.25 m/jaar of meer dan 0.25 m/jaar?
8. Wat is de levensvorm van de soort?
Hydrofyt, helofyt, kruidachtige chamaefyt, epifyt, hemicryptofyt, liaan, phanerofyt, saprofyt, therofyt, parasiet, halfparasiet, houtige chamaefyt, geofyt
9. Indien de soort buiten cultivatie zou groeien, verwacht u dan dat deze alleen onder voedselrijke, vochtige en verstoorde omstandigheden zou kunnen groeien of ook in meer ecotopen?

Ontkieming

10. Heeft het zaad een speciale behandeling nodig om te ontkiemen (zoals een periode van kou)?
11. Kiem de soort in voorjaar, najaar of in beide jaargetijden?

Bloei

12. In welke maand start de bloei?
13. In welke maand eindigt de bloei?
14. Indien de plant niet eenjarig is; na hoeveel jaar gaat deze bloeien?
15. Zijn de bloemen eenslachtig of tweeslachtig? Indien eenslachtig, eenhuizig of tweehuizig?

Bestuiving

16. Kan deze soort aan zelfbestuiving doen? Zo niet; hoe wordt de soort bestoven, door wind of insecten? Indien door insecten, door meerdere soorten of door één specifieke soort?

Zaad

17. In welke maand start de zaadproductie?
18. In welke maand eindigt de zaadproductie?
19. Wat is de lengte van het zaad gemiddeld (in mm)?
20. Hoeveel zaden wordt er ongeveer per plant geproduceerd?
21. Is het zaad aangepast om over lange afstanden te verspreiden? Zo ja, volgens welke methoden (Wind, water, dieren, vogels en/of mensen)?
22. Is er bij deze soort sprake van een zaadbank in de grond? Zo ja; hoelang blijft deze bestaan (<1 jaar, 1-4 jaar of >4 jaar)?

Vergelijking met wilde verwant

23. Vergelijk het gewas met de wilde verwant. Op welke vragen 1-22 scoort de wilde verwant anders? Graag de nummers van de vragen aangeven waarin er verschil is en ook kort wat de richting van het verschil is. Ook graag aangeven als er andere relevante eigenschappen zijn waarin verschil tussen gewas en wilde verwant.
24. Vindt u de genoemde punten relevant voor weediness van het relevante gewas? Welke additionele punten zijn relevant voor weediness?
25. Waarom is uw gewas geen onkruid in Nederlandse omstandigheden?
26. Zijn er eigenschappen die, als je ze verandert, er voor zouden kunnen zorgen dat het gewas zich wel als onkruid gaat gedragen?
27. Heeft u verder nog opmerkingen?

