Alien plants in checklists and floras: towards better communication between taxonomists and ecologists

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The number of studies dealing with plant invasions is increasing rapidly, but the accumulating body of knowledge has unfortunately also spawned increasing confusion about terminology. Invasions are a global phenomenon and comparison of geographically distant regions and their introduced biota is a crucially important methodological approach for elucidation of the determinants of invasiveness and invasibility. Comparative studies of alien floras provide substantial new insights to our understanding of general patterns of plant invasions. Such studies, using information in previously published floras and checklists, are fundamentally dependent on the quality of the assessment of particular species with respect to their taxonomic identity, time of immigration and invasion status. Three crucial decisions should be made when defining the status of a plant species in a given region: (1) whether the taxon is native or alien to that region (origin status); (2) what is its position in the invasion process, i.e., when was it introduced (residence status); and (3) what is the degree of its naturalization and possible invasion (invasion status). Standard floras differ hugely in their treatment of non-native species and those with appropriate categorization of alien species according to their status are rather rare. The present paper suggests definitions of terms associated with plant invasions and places these into the context of floras. Recommendations are outlined on how to deal with the issue of plant invasions in standard floras with the aim of contributing to a better understanding between taxonomists and ecologists and allowing more detailed comparative analyses of alien floras of various regions of the world.

KEYWORDS: Alien, biological invasions, exotic species, hybrid, invasive, native, naturalized, plant invasions, standard floras, terminology, weed

INTRODUCTION: THE IMPOR-TANCE OF PRECISE TERMINOLO-GY IN THE STUDY OF PLANT INVA-SIONS

Invasion ecology is one of the most rapidly developing branches of ecology (Williamson, 1996; Rejmánek & al., in press). Recent developments in this field have brought about the need to standardize terminology (Richardson & al., 2000). The awareness of the importance of biological invasions dates back to De Candolle (1855) and Darwin (1859), but the field was set on firm ground in the middle of the 20th century by the work of Charles Elton (1958), followed in the last quarter of the century by international programs, notably those co-ordinated by SCOPE (Drake & al., 1989) and the Global Invasive Species Programme (GISP; Mooney, 1999; Mooney & Hobbs, 2000; McNeeley & al., 2001). Plant geographers studying plants associated with people have given attention to issues of terminology since the 19th century (Thellung, 1905, 1918/1919; Holub & Jirásek, 1967; Schroeder, 1969), well before invasion ecology was recognized as a subdiscipline of ecology, and before basic knowledge of the processes driving invasions started to be accumulated. The past few decades have seen a rapid increase in the number of studies devoted to plant invasions, but the accumulating body of knowledge has unfortunately also spawned increasing confusion in terminology (Pyšek, 1995; Richardson & al., 2000).

The search for a precise lexicon of terms and concepts in invasion ecology is not driven by concerns of just semantics. Invasions are a global phenomenon and comparison of geographically distant regions and their introduced biota is a crucially important methodological approach for describing observed patterns, and an essential step in the search for elucidation of the determinants of invasiveness and invasibility (Crawley & al., 1996; Goodwin & al., 1999; Rejmánek & al., in press). Unfortunately, the distinction between native and naturalized alien species is not made or even attempted in some recently published checklists (e.g., Dubs, 1998; Balick & al., 2000; Kress & al., 2003). This makes it very difficult not only to assess the degree of "feralization" of individual countries or regions, but also can lead to significantly inflated values for native biodiversity.

Recently, further misunderstandings have been caused by rapidly developing technologies and improved communication via the Internet. The fact that unprecedented quantities of data have accumulated (see Randall, 2002) and are more easily accessible is reflected by the increasing number of comparative studies of alien floras (Rejmánek, 1996; Weber, 1997; Daehler, 1998; Pyšek, 1998; Lonsdale, 1999). Some of these studies have provided substantial new insights in our understanding of general patterns of plant invasions or in correcting generally accepted views (Rejmánek, 1996; Lonsdale, 1999). These papers show the value of including a clearly thought-out list of alien taxa in all standard floras. Moreover, comparative studies of floras are a useful tool for generating hypotheses that can be tested using other approaches (Daehler, 2001a). Such studies, using information in previously published floras and checklists, are fundamentally dependent on the quality of assessment of particular species with respect to their taxonomic identity, time of immigration and invasion status. Ecologists working with a complete flora of a given region rely on the work of taxonomists and plant geographers, especially those producing local and regional floras (Webb, 1985). When using data from such lists, it is technically impossible to check the status of individual species under study when performing comparative studies (but a detailed historical study can lead to the correction of a mistaken species status being copied from one flora to another, see Barbour & Rodman, 1970). We are becoming increasingly worried, for that reason and for the reasons we give below, about generalizations that are drawn from lists of alien species in regional floras.

The quality of data on alien species in *Flora Europaea* (Tutin & al., 1964–1980), a basic source used as data input for comparative analyses on the continental level (Weber, 1997), can be assessed by comparing the treatment of alien taxa in this flora with that in the alien flora of the Czech Republic (Pyšek & al., 2002b), in which very careful attention was given to categorizing alien taxa (Pyšek, 2003). There are 332 naturalized species reported in *Flora Europaea* from the former Czechoslovakia (Weber, 1997). The issue is complicated by the fact that these records also include the territory

that is now Slovakia; excluding species found only in that country (Gojdicová & al., 2002) and planted species which have never been reported escaping from cultivation, leaves 312 species relevant to the Czech Republic. Among these, there are seven species now considered native and 15 obviously erroneous records. In total, there are 290 species correctly identified in Flora Europaea as aliens to the Czech flora based on current knowledge. Major inconsistencies and discrepancies are associated with the assessment of invasion status. Flora Europaea claims to include only "aliens that are effectively naturalized" but 161 species of the 290 reported are not considered naturalized in the Czech Republic (Pyšek, 2003). Moreover, the recent checklist of alien flora of the Czech Republic gives 229 naturalized neophytes (Pyšek & al., 2002b) of which only 118 are on the *Flora Europaea* list. Even considering that the number of alien species in the Czech Republic has been increasing (Pyšek & al., 2003) and that new species have appeared since the publication of Flora Europaea (Tutin & al., 1964-1980), there are 111 naturalized species (48.5% of those currently known) missing from Flora Europaea.

There is no reason to believe that this situation is different in other countries. Given the lack of confidence that can be attached to the invasion status in such data, there is a danger that inconsistencies and discrepancies are unknowingly carried over to analyses based on species numbers reported for particular countries (e.g., Weber, 1997). The concept of alien species in Flora *Europaea* obviously suffers in that at the time of its preparation the issue of biological invasions was not as intensively studied nor were knowledge bases as well developed as they are now; the treatment of alien species could therefore not have been as thorough and comprehensive as is now possible with new insights. It is therefore perhaps unfair to judge this work by current perspectives. However, some recent floras have not made much progress with respect to approaches to classification of alien plants. In the new Flora of North America (Stuckey & Barkley, 1993), numerous rather vaguely defined terms are used and biological and sociological criteria are confused.

Three crucial questions should be asked when dealing with alien plants: (1) whether the taxon is native or alien to the region (origin status), (2) what is its position in the invasion process, i.e. when was it introduced (residence status), and (3) what is the degree of its naturalization and possible invasion (invasion status). The first issue is most relevant with respect to floras as this information is standard in such works. In his pioneering work, Webb (1985) postulated several useful criteria for presuming native status that were later extended by Preston (1986) and applied by Smith (1986) to annual *Bromus* species; most of these criteria are still relevant. They include palaeobotanical information as the only certain evidence of native status, historical records as the only evidence of introduction, and a number of other helpful criteria. These include ease of naturalization elsewhere, character of the overall distribution area, type of habitat, and relationship with biota on other trophic levels (some alien plants were reported to harbor less phytophagous insects than native species or to have brought their herbivores from the primary distribution range; Preston, 1986). In non-tropical zones, many species are easily classified as native or introduced as they have a continuous fossil record since at least the last glacial period. Even in the absence of such evidence, many species can be judged to be native beyond any reasonable doubt on the basis of historical, phytogeographical and ecological evidence. For example, many species were recorded in their current localities by early botanists, grow in natural or semi-natural habitats, and their presence in the area is consistent with their wider total distribution (Preston & al., 2002). Genetic studies are a powerful tool for resolving problems with difficult species (Neuffer & Linde, 1999; McCauley & Ballard, 2002), and in the future they may be expected to provide more precision to our assessment of the status of particular species¹. However, decisions now often have to be made on the basis of the balance of evidence, and cannot always be proven beyond reasonable doubt (Preston & al., 2002).

Assessing species residence and invasion status constitutes an even bigger problem, probably because the concepts surrounding these issues have only been carefully considered by ecologists relatively recently compared to the question of whether a species is native or alien. To understand this, historical circumstances must be reviewed. In the early 20th century, the classification of alien plants was given most attention in Central Europe, and complicated systems using a large number of terms were developed, based on the date of species arrival, degree of naturalization, and the habitat type invaded (Thellung, 1905; Holub & Jirásek, 1967; Schroeder, 1969). Such classification systems have not received wide attention in English-speaking countries where the most intensive research on plant invasions started to be carried out in the last quarter of the 20th century, primarily for practical reasons (see the discussion in Richardson & al., 2000: 96). Plant invasions represent the most serious threats in those regions of the world that were under the influence of British colonization (di Castri, 1989). Central Europe is much less prone to invasions, at least in terms of rapid and dramatic impacts (Pyšek & al., 2002a). We suspect that the complicated

terminology of Central European classification, which used a large number of terms mostly derived from Greek, was the primary reason that this terminology has not been more widely accepted by current researchers (Pyšek, 1995; Richardson & al., 2000; see Table 1 for a comparison of the Central-European system with that suggested here), even though Thellung gave English translations of his terms. As a consequence, several different terms were (and are still) used to designate residence and invasion status without proper definitions and attempts to relate them together (Pyšek, 1995; Richardson & al., 2000).

In a previous paper, we demonstrated that relatively few terms are needed to characterize, with fair precision, a species' residence and invasion status (Richardson & al., 2000). We based the suggested terminology primarily on the degree of naturalization. If the terms defined in that paper are combined with traditionally used criteria (such as time of introduction and habitat type in which an alien species occurs), sufficient information about the alien species in a given region can be achieved. In the present paper, we revisit the definitions proposed by Richardson & al. (2000), expand some of them, and place these into the context of floras. In addition, attention is paid to the issue of origin status which was not discussed in the previous paper.

CURRENT APPROACHES TO THE CLASSIFICATION OF ALIEN PLANTS

Distinguishing native from alien. — There is wide agreement that plant invasions, as a direct and indirect consequence of human activities, are related to human activity. It seems plausible to reserve the term "invasion" for situations where the distribution and abundance of plants changes as a result of human activities. For other processes, unrelated to human activities, different terms should be used. There are two other ecological situations where the term invasion is, in our opinion, inappropriately used. The first concerns changes in distribution ranges after the retreat of glaciation. For such processes, we suggest that the terms "migration", "spread", "range expansion" or "range extension" be used. The second example of a misleading use of the term invasion concerns species that increase their distribution and colonize new habitats in a geographical area where they are native. These habitats are mostly of anthropogenic origin. This means that such distribution changes are dependent on human activities (as are inva-

¹On the other hand, improving knowledge of genetic variation with respect to invasions brings about the need to deal with a new problem of introductions at the genotype level, for which the term "cryptic invasion" was suggested (Saltonstall, 2002). In such cases, the terminological background is the same as when dealing with taxa.

sions) but the fact that such species are native (they have localities of native occurrence within the same area) makes it inappropriate to use the term "invasion". Species spreading under such circumstances should be termed "expansive" and the process "expansion" (Prach & Wade, 1992).

Terminological misunderstandings can be partly caused by different perceptions of plant invasions by particular biological disciplines and viewpoints. As shown by Rejmánek (1995), plants encroaching in habitats in which they were not present before can be assessed from the ecological point of view (and termed colonizers) or from the biogeographical (invaders, or alien plants in a more general sense) or anthropocentric (termed weeds, pests, etc.) points of view (Fig. 1). We argue that in biological invasions, the biogeographical approach should be preferred (Rejmánek, 1995, 2000). Many recent checklists and catalogues follow this approach (Pyšek & al., 2002b; Essl & Rabitsch, 2002; Preston & al., 2002; Klotz & al., 2002), and once it is determined that a plant has a native locality in the territory of the country, it is excluded from the national list of aliens even if its occurrence in most of localities is secondary. This is partly for technical reasons; when taking the ecological point of view on invasions (therefore adopting the occurrence in secondary habitats as a criterion for including a species among aliens), the majority of the flora would appear on such a list since in contemporary highly disturbed landscapes many native plants occur at least partly in disturbed and human-made sites. In the same vein, a native plant (or a hybrid between two native plants), is still native, even if it now occurs only in secondary habitats. Consequently, in our view, habitat type is an important taxon characteristic, but not a criterion for decision about origin status. The criterion should be purely the involvement of people in moving the species from one region to another.

When preparing national lists, it therefore seems reasonable to consider the study area as a whole, so that a species that is native anywhere within this area is regarded as native (Preston & al., 2002). It can be argued that political boundaries are not an ideal framework because they do not correspond to biological and ecological barriers that are crucial in plant invasions (Richardson & al., 2000). This problem is more pronounced in large countries, such as Australia and the U.S.A., where many species from east/west coasts are as foreign on the other coast as species from another continent. Ideally, alien and native occurrence in concrete localities within a region should be distinguished, but such data are not available for large species sets (many floristic papers and herbarium sheets only give geographically defined localities with no specification of habitat). Nonetheless, to start data collation within new projects with this in mind



Fig. 1. Approaches used to classify plants encroaching in habitats and territories where they were not present before. Weeds, colonizers and aliens are three different concepts reflecting anthropocentric (weeds are plants growing where they are not wanted), ecological (colonizers appear early in succession), and biogeographical (alien species encroach the areas where they are not native) viewpoints. Adapted from di Castri (1990), Rejmánek (1995, 2000), and Williamson (1993, 1996). In the Californian flora, for example, there are at least 1150 colonizers, 1050 naturalized species, 670 weeds, and 380 species are within the overlap of all three groups, i.e., early successional alien weeds (for more details with examples see Rejmánek, 2000).

should be highly encouraged. To our knowledge, there is only one source with information on the distribution of a complete alien flora categorized in such a way: Preston & al. (2002) in their *New Atlas of the British and Irish flora* give for each species precise information on the number of alien and native occurrences recorded. Such information greatly improves the potential for analyses of alien floras because, in association with environmental characteristics, the data can be examined on a finer scale. On the other hand, working at a country level (when comparing number of regions or countries) makes it possible to obtain synthetic environmental and economic parameters that are usually recorded at the scale of regions, states, or other political (rather than biogeographic) boundaries.

Even if we agree that biological invasions are human induced, it is crucial to define the role of people. The definition can be based either on "what is alien?" or "what is native?", from which the reasoning follows that what is not native is alien and vice versa. Which approach is used makes an important difference, potentially leading to serious misunderstanding. Where the definition is built around the term alien, an alien taxon is simply one that would not be present in the area had it not been for the

Box 1. Suggestions for a standardized terminology for alien plants.

It should be borne in mind that the definitions of status given here will not fit perfectly in every case, since the stages in the invasion process represent a continuum. In the literature, more terms can be found reflecting the continuum between particular stages of the process, e.g., "surviving" (Macpherson & al., 1996) or "long-term casuals" (Clement & Foster, 1994). Given that precise definitions are provided by those authors, these categories are legitimate but may introduce additional difficulties when deciding about invasion status. Our aim is to provide definitions that fit most cases, with guidelines on how deviations from standard criteria should be noted. For each term, a definition is provided followed by frequently used synonyms (where applicable) and by guidelines on interpretation (where necessary). For applicability of terms with respect to the origin status see Table 2.

Native plants

Synonym: indigenous plants.

- *Definition*: Taxa that have originated in a given area without human involvement or that have arrived there without intentional or unintentional intervention of humans from an area in which they are native.
- Interpretation: This definition excludes products of hybridization involving alien taxa since "human involvement" in this case includes the introduction of an alien parent.

Alien plants

Synonyms: exotic plants; introduced plants; non-native plants; non-indigenous plants.

- *Definition*: Plant taxa in a given area (see below) whose presence there is due to intentional or unintentional human involvement, or which have arrived there without the help of people from an area in which they are alien (Fig. 2).
- *Interpretation*: Taxa can be alien to any definable area, e.g., continents, islands, bio- or ecoregions, or any political entity (e.g., countries, states, provinces). Human involvement here does not include habitat changes, global warming, atmospheric nitrogen fertilization, acid rain, etc. Native species that change their geographical range due to these processes should not be considered aliens unless there is clear evidence of significant leaps in distribution attributable to human-aided dispersal of propagules. For the purpose of particular studies, a geographic modifier should be included of how far a taxon has to be moved by human activities from the border of its native distribution to be considered alien. It would normally be arbitrary where political boundaries are involved, and natural where biogeographic boundaries exist, e.g., between islands and mainlands, on the borders of phytogeographical regions or wherever there are natural barriers. The term alien also includes all non-native taxa under cultivation. Many alien taxa that currently are not casual aliens, naturalized plants or invasive plants, may become such in the future.

Casual alien plants

- Synonyms: Given the difficulties associated with definition of casual plants, there are no consistenly used synonyms in the literature. The term "subspontaneous" can be found in the French literature. In the original sense of Thellung (1918/1919) this term refers to species that escaped from cultivation and occur as casuals outside cultivation. However, the term is now also used for native species which, recently and at the regional scale, have disappeared and were re-introduced through human activities. Other synonyms or partial synonyms include "waifs" (Hickman, 1993), "occasional escapes" (Munz, 1968), and "ephemeral taxa" (Elven & Elvebakk, 1996). They correspond to De Candolle's (1855) original usage of the term "adventive", that has been later used in much broader sense (Muhlenbach, 1979; Burda, 1991; Provost, 1998). At present, the usage of this term is inconstent; it is sometimes used to mean casual, sometimes to mean alien, and occasionally to mean naturalized.
- *Definition*: Alien plants that may flourish and even reproduce occasionally outside cultivation in an area, but that eventually die out because they do not form self-replacing populations, and rely on repeated introductions for their persistence.

Naturalized plants

Synonym: established plants.

- *Definition*: Alien plants that sustain self-replacing populations for at least 10 years without direct intervention by people (or in spite of human intervention) by recruitment from seed or ramets (tillers, tubers, bulbs, fragments, etc.) capable of independent growth.
- *Interpretation*: Naturalized plants do not necessarily invade natural, semi-natural or human-made ecosystems. How long a species must persist to be considered naturalized is inevitably arbitrary, and hence affects how the definition should be used in practice. In *Flora Europaea* (Tutin & al., 1964–1980) a period of 25 years is used. We believe that a 10-year period reasonably reflects possible negative effects of short-term "catastrophic events" such as climatic extremes, outbreak of pests and pathogens, etc. A species may form self-replacing populations for several years and then go extinct; such species should still be termed casual. Taxa persisting in sites where they were planted (after cultivation has ceased) represent a special category, but they can be classified within the current scheme as either casual or naturalized.

Box 1 (continued).

Invasive plants

Definition: Invasive plants are a subset of naturalized plants (Fig. 2) that produce reproductive offspring, often in very large numbers, at considerable distances from the parent plants, and thus have the potential to spread over a large area.

Interpretation: Approximate scales: > 100 m in < 50 years for taxa spreading by seeds and other propagules (for dioecious taxa that rely exclusively on seeds for reproduction, this applies only after the introduction of both sexes); > 6 m in 3 yrs for taxa spreading by roots, rhizomes, stolons, or creeping stems. Taxa that spread previously, but do not spread currently because the total range of suitable habitats and landscapes has been occupied, should still be termed invasive because local eradication will undoubtedly lead to re-invasion. Many alien taxa that are not classified as "invasive" by the criteria above may become invasive in the future, given time to reach optimum habitats, to make adaptive genetic changes, or when key mutualist partners arrive in their new range; some taxa may also become invasive because of the introduction of new genotypes.

Transformers

- *Synonyms*: Transformers are essentially equivalent with edificators, a term used in European, especially Russian literature. Edificators are defined as "environment forming plants" (Braun-Blanquet & Pavillard, 1922; Mirkin & Naumova, 1998).
- *Definition*: A subset of invasive plants (not necessarily alien) that change the character, condition, form or nature of ecosystems over a substantial area. (Substantial means relative to the extent of that ecosystem.)
- *Interpretation*: The term is an ecological one; a plant can be a transformer without receiving human attention by way of economic concern or control efforts. Several categories of transformers may be distinguished: excessive users of resources (water, light, oxygen), donors of limiting resources (nitrogen), fire promoters/suppressors, sand stabilizers, erosion promoters, colonizers of intertidal mudflats/sediment stabilizers, litter accumulators, salt accumulators/redistributors, etc. (see Richardson & al., 2000, table 1, for examples of species).

Weeds

- *Synonyms*: pests; harmful species; problem plants; noxious plants. The last term is often used, particularly in U.S.A., for a subset of weedy taxa, whose control/eradication is mandatory.
- Definition: Plants (not necessarily alien) that grow in sites where they are not wanted and which have detectable economic or environmental impact or both.

Interpretation: Although the term "weed" invokes no biogeographic concepts and has very limited value in floras, we consider it useful to include it here since economic and environmental effects are increasingly receiving attention in studies on invasive plants. The term is anthropocentric, and a plant is considered a weed if it interferes with human objectives. The terms "environmental weeds" (Humphries & al., 1991; Randall, 1997) or "species of environmental concern" (e.g., Space & al., 2003) are used for alien plant taxa that invade natural vegetation, usually adversely affecting native biodiversity and/or ecosystem functioning.

translocating effect of people². A frequently used alternative is based on the nativeness of the taxon in question, i.e., a native taxon is one that evolved (originated) in the region. As Webb (1985) pointed out, an important addition must be made with regard to time scale; a species that was native in the area before the last glaciation, then retreated and was re-introduced by people, should not be considered native now. A good example is *Rhododendron ponticum* in Ireland (Godwin, 1975).

This issue appears especially relevant when classifying products of hybridization involving alien species. There are conflicting views on this. Some authors consider hybrids that have arisen in a region as native to that region regardless of the place of origin of parental species (Stace, 1991; Macpherson & al., 1996; Preston & al., 2002). They argue that species resulting from humanmediated genetical processes are "native" due to their evolution in the given region and because they lack an alternative native range. For example, most British floras count crosses between natives and aliens as native if they have arisen in the British Isles. Similarly, in Washington State, U.S.A., two new tetraploid *Tragopogon* species (*T. miscellus*, *T. mirus*) originated through hybridization of completely alien, European material (Ellstrand & Schierenbeck, 2000). Undoubtedly, this is the place of their origin. *Tragopogon mirus* was originally classified as "sensitive", i.e., vulnerable to declining, by the Washington Native Plant Society (Washington Natural Heritage Program, 1982). In a later edition, both taxa are marked as "more abundant and/or less threatened in

²A substantial effect of humans in present landscapes is habitat change. A specification of "translocating effect", i.e., humans introducing and moving plants from one region to another, must be made here to exclude native plants spreading in secondary habitats such as the well-known example of Dittrichia viscosa in the Mediterranean Basin (Wacquant, 1990) and other so-called "apophytes" (Holub & Jirásek, 1967). Habitat change should be therefore excluded from the "had it not been for the humans" as a classification criterion.



Fig. 2. Hierarchical scheme for the suggested classification of alien plants (see Box 1 for definitions of terms). Note that the categories at each level are mutually exclusive with the exception of "cultivated" and "outside cultivation", and "weeds" and "transformers", respectively, which can overlap. The scheme assumes a negative effect of transformers but their influence could, hypothetically at least, also be beneficial. For example, it is conceivable that completely degraded soils in Africa can be restored using exotic species of pines or eucalypts. An overlap of "not harmful" and "transformers" cannot be therefore excluded in such special situations. Note that both "weeds" and "transformers" can be also native taxa.

Washington than previously assumed" (State of Washington Department of Natural Resources, 1984) and in 1997, they were deleted from the list as no longer endangered (Washington Natural Heritage Program, 1997). Such dynamics of population growth and spread seem to be, however, more typical of alien rather than native taxa.

There is currently no clear agreement on how to treat products of hybridization involving alien species. However, disregarding re-introductions (Guerrant & Pavlik, 1998), we believe that it is inconsistent to call a species "native" if it would not be present in the region without human intervention (which may be indirect, as is the case of a spontaneous hybrid when one or both parents were introduced). We consider them alien in the sense of not having been in the region before agriculture (Smith, 1986; Williamson, 2002). According to our approach, species like Senecio cambrensis (Abbott, 1992) or Spartina anglica (Williamson, 1996) are aliens in Britain and Tragopogon miscellus and T. mirus in the State of Washington. The same approach was adopted by Crawley & al. (1996) who define natives as "species that would be present without human intervention". Kowarik (2003) suggests treating the products of hybridization involving alien plants as an additional subset of alien species. The analysis of the Czech flora shows the relevance of this species group. The list includes 49 hybrids with archaeophytes (introduced before 1500 AD), and 69

with neophytes (introduced after that date) among the parental species (Pyšek & al., 2002b). We believe that since invasions are a human-related phenomenon, the "had-it-not-been-for-people" reasoning is more appropriate for the definition than the "where-it-evolved" approach.

The issue of hybrids includes the special situation of plants that do not have a native distribution range and/or native habitats. This does not apply only to hybrids. As has been suggested for annual bromes, some species are not native in any primary habitat and perhaps never have been. Some bromes that are supposed to be native in Asia are known only as introduced plants, e.g., in Europe. They have never been found in SW Asia, which is the center from which the current adaptive radiation of *Bromus* annuals began (Smith, 1986). For such cases, the term "homeless plant" was coined by Zohary (1962). In flora analyses, such taxa should be labelled as "origin unknown" as is also the case with many old cultural plants kept in cultivation for millennia so that their wild ancestors are now uncertain (Clement & Foster, 1994).

In some cases there will be native populations that have been infiltrated by alien genes, from garden plants or elsewhere. Decisions on status will then be difficult and need to be based on the best evidence available. In other cases it may be possible to distinguish native and alien populations of the same species in one country as, for instance, in many cases in Preston & al. (2002), such as *Meconopsis cambrica*, even though there will usually be some hybrids.

Residence status. — Residence status is a characteristic providing information about residence time, i.e., how long an alien species has been present in the region. Invasion status is, in general, closely related to residence time as shown for several data sets from various parts of the world (Pyšek & al., 2003; Wu & al., 2003). This is because invasions are often triggered by rare events; the longer a plant is present at a given locality, the better its chance of experiencing conditions conducive to invasion (Rejmánek & al., in press). Knowledge of the residence status of a species in a region is important since assessments of a species' invasiveness are sometimes made after too short a residence time. The likelihood of an erroneous assessment (e.g., labelling an invasive species in its lag phase as "safe") after a short residence time is very high (Rejmánek & al., in press).

In Central Europe, alien species are traditionally classified as archaeophytes if introduced before the year 1500, and neophytes if introduced after that date (e.g., Holub & Jirásek, 1967; Schroeder, 1969; Pyšek & al., 2002b). The separation between natives and archaeophytes is sometimes difficult and relies on a combination of palaeobotanical, archaeological, ecological and historical evidence (Preston & al., 2002). Accumulating

Table 1. Comparison of the terminology for alien plants that has been traditionally used in Central-European classification schemes (based on Holub & Jirásek, 1967) with the one suggested in the present paper (based on Richardson & al., 2000). Criteria used by Holub & Jirásek (1967) for the classification of particular categories are indicated: T = time of immigration, M = means of introduction, H = type of encountered habitat. Note that in our scheme, neophytes and archaeophytes are sudivisions of both hemerophytes and xenophytes (see Pyšek & al., 2002b).

Term in Holub &			
Jirásek (1967)	Criteria	Explanation	As expressed using the terminology here
Anthropophytes		introduced by people regardless of time and means	alien
I. Hemerophytes	М	introduced intentionally	any intentionally introduced alien
1. Ergasiophytes	MH	found only in cultivation	cultivated alien
 Ergasiophygo- phytes 	MH	found in cultivation and occasionally escaping	intentionally introduced casual alien
3. Ergasiolipophytes	s MH	formerly planted, currently occurring in the territory without need of human intervention	intentionally introduced alien, naturalized or invasive
II. Xenophytes	М	unintentionally introduced	any unintentionally introduced alien
1. Archaeophytes	MT	unintentionally introduced before ca. 1500 ¹	alien introduced before ca. 1500, both deliberately or accidentally, regardless of invasion status
2. Neophytes	MT	unintentionally introduced after ca. 1500	alien introduced after ca. 1500, both deliberately or accidentally, regardless of invasion status
(a) Ephemerophyte	s MTH	occurring temporarily in human-made habitats	casual alien introduced after ca. 1500
(b) Epekophytes	MTH	established in human-made habitats	alien introduced after ca. 1500, naturalized or invasive in human-made habitats
(c) Neoindigeno- phytes ²	MTH	established in the region, occurring in human-made habitats and penetrating to natural habitats, too	alien introduced after ca. 1500, naturalized or invasive in seminatural and/or natural habitats

¹Approximate date corresponding to the discovery of America (1492).

²Some authors use the term "agriophytes" (Schroeder, 1969; Lohmeyer & Sukopp, 1992) for this category, which is sometimes further divided into "holoagriophytes" (in natural vegetation) and "hemiagriophytes" (in seminatural vegetation; see, e.g., Kornas, 1990).

palaeobotanical evidence is improving the precision and the determination of a species' residence status (Pyšek & al., 2002b). Both archaeophytes and neophytes are usually absent from the fossil record in the last glacial period, the late glacial and the early post-glacial. Archaeophytes are often known from archaeological evidence to have been present in prehistoric times (Preston & al., 2002). Habitat is also an important criterion for deciding whether a species is an archaeophyte or neophyte. Since many archaeophytes now only occur in human-made habitats, we can ask, on the basis of the knowledge of their ecology, whether we can identify their potentially native habitat in the landscape before it was affected by people (Pyšek & al., 2002b).

The archaeophyte/neophyte concept has been recently adopted in the British Isles by Preston & al. (2002). However, its use there differs from the traditional one in that it relates residence status to invasion status³. We believe that it is better to separate residence status and invasion status. By merging them in floras we lose the possibility of classifying archaeophytes that are kept in cultivation for millennia but only escape occasionally as casuals, as is the case with some trees (Pyšek & al., 2002b).

In other parts of the world, e.g., Australia, a distinction is sometimes made between taxa that arrived before or after European colonization (Kloot, 1987). In Hawaii, separating species introduced by Polynesians (there are at least 14 of them) before Captain James Cook's "discovery" of the islands in 1778 corresponds to this approach (Webster, 1992). A similar approach is adopted for other Pacific islands (Florence & al., 1995; Waldren & al., 1999).

Invasion status. — In the literature on plant invasions, invasion status is complicated because: (a) there is a continuum between particular categories; and (b) its

³According to Preston & al. (2002), archaeophytes and neophytes are introduced species that are present in the wild as naturalized populations. An archaeophyte is a plant that became naturalized before AD 1500. A neophyte is one that was first introduced after 1500 or was only present as a casual before 1500 and is naturalized now only because it was re-introduced subsequently. In contrast to archaeophytes and neophytes, a casual is a plant that is present only as populations that persist outside cultivation for periods of more than approximately five years, and such a species is therefore dependent on constant re-introduction.

Table 2. The applicability of some terms discussed in this paper to native and alien taxa. "+" indicates apropriate use; "-" shows where the usage is inappropriate.

Plants	Native	Alien
Cultivated	+	+
Outside cultivation	+	+
(Range) expansion	+	-
Casual	-	+
Naturalized	-	+
Invasive	-	+
Weeds	+	+
Transformers	+	+

classification to a large extent depends on researchers' personal perception of the species and processes studied. Differing opinions can be often found as to whether the species is casual or naturalized, and only naturalized or also invasive. Nonetheless, it seems plausible to create a theoretical framework with precise definitions to which real situations can be related.

Many invasive species have substantial impacts in their new range. However, some recent efforts to base the definition of the term "invader" on impact as a measure (Davis & Thompson, 2000) seem unfortunate to us, especially as far as economic effects are concerned (Rejmánek & al., 2002). Introducing practical reasons outside of the discipline of ecology (Davis & Thompson, 2001) or even political aspects (such as the U.S. President's Executive Order No. 13112, http://invasivespecies.gov/laws/exeorder.shtnl) makes understanding between workers in the field even more difficult. We agree with Daehler (2001b) that defining invaders as those species with the largest impacts is an exercise in subjectivity that will be unlikely to contribute to clarity. In our view, the invasive status of a species at a given locality should be based on measures of population growth and spread in the new region. Such a definition captures a general ecological process that can be confirmed with simple measurements, leading to greater agreement among ecologists, and greater progress in understanding invasions as ecological phenomena. Several recent textbooks (Gurevitch & al., 2002; Mac-Donald, 2003) define the term "invasion" without considering impact as a criterion.

In a previous paper (Richardson & al., 2000), we analysed in detail the way various terms relating to the invasion status are used in the literature and suggested a simple and consistent terminology. The scheme presented in Box 1 is based on these definitions but improves their precision, and also offers a definition of native.

CONSIDERING BIOLOGICAL INVA-SIONS IN CHECKLISTS AND STAN-DARD FLORAS

"Standard floras", e.g., those included in Frodin (2001), differ hugely in their treatment of non-native species. Some floras simply leave out all alien species; this is a pity, but at least we know where the authors stand. Many others (e.g., Goldblatt & Manning, 2000) include some alien taxa (often a haphazard assortment), but provide inadequate descriptions of the criteria used to decide which alien taxa to include and which to leave out or do not indicate this at all (Rejmánek, 2001). Floras with appropriate categorization of alien species according to their origin, invasion and residence status (e.g., Fournet, 2002) are rather rare. This is especially worrisome and misleading.

In the following paragraphs, we attempt to outline recommendations on how taxonomists should deal with the issue of plant invasions in standard floras. Consideration of this would contribute to a better understanding between taxonomists and ecologists and allow for more detailed comparative analyses of alien floras of various regions of the world.

(1) Close cooperation with ecologists and plant geographers studying alien plants of a given territory is necessary. Reliable checklists of alien plants have started to appear recently for many European countries (e.g., Clement & Foster, 1994; Essl & Rabitsch, 2002; Pyšek & al., 2002b; Klotz & al., 2002) and the information they contain should be incorporated in national floras and identification keys (e.g., Rothmaler & al., 2002). Such cooperation would make it possible to include not only naturalized but also casual aliens, which is highly desirable. These species can be treated in lesser detail but should not be omitted since they represent valuable information to be used in comparative studies. Horticultural floras (Walters & al., 1984–1989; Cullen & al., 1995-2000; Spencer, 1995-2002) can also profit from incorporating this information, leading to an updated and thorough treatment of alien species, because these floras can point to planted taxa that are escaping from cultivation and that are naturalizing.

(2) As outlined by Palmer & al. (1995), the origin status of each species should be clearly indicated. Clear definitions of the terms used or a reference to the source of the definitions should always be given. The area to which species are alien should be explicitly indicated (e.g., country, continent or its part). The geographic origin of alien species may also be useful to some flora users, and source data for determining status or origin should be cited (Palmer & al., 1995). This information, however, is often lacking even in most recent treatments of non-native taxa (Hrusa & al., 2002). The parentage of hybrid taxa should be clearly indicated if an alien species is involved. We hope this paper indicates that although the botanical community may feel confident about what is native, alien, archaeophyte or invasive, this may be a rather complicated issue and the terms are understood in different ways.

(3) A conservative approach should be preferred when attributing alien status to a species. Critical evaluation of past records is needed. Doubtful records, sometimes listed without evidence from one flora to another, should be excluded. On the other hand, once a declaratively complete work on the alien flora of any territory has been published, it is tempting for future researchers to start with that and pay less attention to scattered information sources from earlier times. This brings the danger that most of what is not included in such a "complete" treatment might be overlooked in the future (Pyšek & al., 2002b).

(4) The year of the first report of an alien taxon should be given where known. This provides important information for analyses since many characteristics of alien plants are related to residence time (Pyšek & al., 2003; Wu & al., 2003).

(5) Another extremely important piece of information that should be given in regular floras is the most recent year that the taxon was collected, or at least recorded. Some floras (Rhoades & Klein, 1993) or web checklists (Cholewa, 2002) provide valuable information in this respect. Many casuals (or even naturalized species that have only naturalized in one location) disappear after some time and some floras still treat them as present. For example, there is solid evidence in the Czech alien flora that of 817 casuals, 231 disappeared and were never reported again (Pyšek & al., 2002b). Similarly, in the Staten Island flora, there are 159 non-native species reported in 1879 and 1930 that have not been observed recently (Robinson & al., 1994). Although it is very difficult to state conclusively that a taxon is absent (i.e., extinct in the region), the most recent record can give the reader the option of, for example, ignoring all records that have not been confirmed in the last 50 or 100 years.

(6) Mode of introduction, if known, should be stated (introduced as ornamental, timber, fuelwood crop, medical, for erosion control, bird seed, forage, aquarium plant, accidental with crop seed, accidental with nursery stock, etc.—see e.g., Matthei, 1995; Clement & Foster, 1994; Ryves & al., 1996). Taxa persisting after cultivation should be explicitly noted, where this information is known (see e.g., Clement & Foster, 1994; Ryves & al., 1996; Pyšek & al., 2002b).

(7) An ecologically useful piece of information is whether an alien taxon invades natural/seminatural plant communities or whether it is found only in disturbed areas. Some phytosociological manuals (Oberdorfer, 1994) and recently published floras already provide such data (Jonsell, 2000; Lesica, 2002). Lists of associated species (e.g., Ertter & Bowerman, 2002) can partly substitute or complement this information.

(8) A classification of all the alien species within a given territory, unequivocally completing all the criteria, can usually not be achieved. If the information is missing or the evidence on species status appears to be inconclusive, the uncertainty should be explicitly stated (see, e.g., Clement & Foster, 1994; Preston & al., 2002). For example, around 10% of the species in Clapham & al. (1987) have qualifiers like "possibly" or "probably" on the status. Statements like "probably native", "naturalized and probably invasive", etc., may be, temporarily, the most honest way of classifying some of the taxa.

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LITERATURE CITED

- Abbott, R. J. 1992. Plant invasions, interspecific hybridisation and the evolution of new plant taxa. *Trends Ecol. Evol.* 7: 401–405.
- Balick, M. J., Nee, M. H. & Atha, D. E. 2000. Checklist of the Vascular Plants of Belize. New York Botanical Garden Press, New York.
- Barbour, M. G. & Rodman, J. E. 1970. Saga of the West Coast sea-rockets: *Cakile edentula* ssp. *californica* and *C. maritima. Rhodora* 70: 370–386.
- Braun-Blanquet, J. & Pavillard, J. 1922. Vocabulaire de Sociologie Végétale. Imp. Lemaire-Ardres, Montpellier.
- Burda, R. I. 1991. Antropogennaia Transformacia Flory. Naukova Dumka, Kiev.
- Cholewa, A. F. 2002. Annotated Checklist of the Flora of Minnesota. [http://www.cbs.umn.edu/herbarium/checklis2.htm].
- Clapham, A. R., Tutin, T. G. & Moore, D. M. 1987. Flora of the British Isles, ed. 3. Cambridge Univ. Press, Cambridge.
- Clement, E. J. & Foster, M. C. 1994. Alien Plants of the British Isles. A Provisional Catalogue of Vascular Plants (excluding grasses). Botanical Society of the British Isles, London.
- 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. B* 351: 1251–1259.
- Cullen, J., Alexander, J. C. M., Brady, A., Brickell, C. D.,

Green, P. S., Heywood, V. H., Jørgensen, P.-M., Jury, S. L., Knees, S. G., Leslie, A. C., Mathews, V. A., Robson, N. K. B., Walters, S. M., Wijnands, D. O. & Yeo, P. F. (eds.). 1995. *The European Garden Flora. Vol. 4. Dicotyledons (Part II).* Cambridge Univ. Press, Cambridge.

- Cullen, J., Alexander, J. C. M., Brickell, C. D., Edmondson, J. R., Green, P. S., Heywood, V. H., Jørgensen, P.-M., Jury, S. L., Knees, S. G., Mathews, V. A., Maxwell, H. S., Miller, D. M., Nelson, E. C., Robson, N. K. B., Walters, S. M. & Yeo, P. F. (eds.). 1997. *The European Garden Flora. Vol. 5. Dicotyledons (Part III)*. Cambridge University Press, Cambridge.
- Cullen, J., Alexander, J. C. M., Brickell, C. D., Edmondson, J. R., Green, P. S., Heywood, V. H., Jørgensen, P.-M., Jury, S. L., Knees, S. G., Maxwell, H. S., Miller, D. M., Nelson, E. C., Robson, N. K. B., Walters, S. M. & Yeo, P. F. (eds.). 2000. The European Garden Flora. Vol. 6. Dicotyledons (Part IV). Cambridge University Press, Cambridge.
- Daehler, C. C. 1998. The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. *Biol. Conserv.* 84: 167–180.
- Daehler, C. C. 2001a. Darwin's naturalization hypothesis revisited. *Amer. Naturalist* 158: 324–330.
- Daehler, C. C. 2001b. Two ways to be an invader, but one is more suitable for ecology. *Bull. Ecol. Soc. Amer.* 82: 206.
- Darwin, C. 1859. On the Origin of Species. Murray, London.
- Davis, M. A. & Thompson, K. 2000. Eight ways to be a colonizer, two ways to be an invader: A proposed nomenclature scheme for invasion ecology. *Bull. Ecol. Soc. Amer.* 81: 206.
- Davis, M. A. & Thompson, K. 2001. Invasion terminology: Should ecologists define their terms differently than others? No, not if we want to be of any help! *Bull. Ecol. Soc. Amer.* 82: 206.
- De Candolle, A. P. 1855. Géographie Botanique Raisonné, vol. 2. V. Masson, Paris.
- di Castri, F. 1989. History of biological invasions with special emphasis on the Old World. Pp. 1–30 in: Drake J. A., Mooney, H. A., di Castri, F., Groves, R. H., Kruger, F. J., Rejmánek, M. & Williamson, M. (eds.), *Biological Invasions: A Global Perspective*. John Wiley & Sons, Chichester.
- di Castri, F. 1990. On invading species and invaded ecosystems: the interplay of historical chance and biological necessity. Pp. 3–16 in: di Castri, F., Hansen, A. J. & Debussche, M. (eds.), *Biological Invasions in Europe and the Mediterranean Basin.* Kluwer Academic Publishers, Dordrecht.
- Drake, J. A., Mooney, H. A., di Castri F., Groves R. H., Kruger F. J., Rejmánek, M. & Williamson, M. (eds.). 1989. Biological Invasions: A Global Perspective. John Wiley & Sons, Chichester.
- **Dubs, B.** 1998. *Prodromus Florae Matogrossensis*. Betronas Verlag, Küsnacht, Switzerland.
- Ellstrand, N. C. & Schierenbeck, K. A. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants. *Proc. Natl. Acad. Sci., U.S.A.* 97: 7043-7050.
- Elton, C. 1958. The Ecology of Invasions by Animals and Plants. Methuen, London.
- Elven, R. & Elvebakk, A. 1996. Part 1. Vascular plants. In:

Elvebakk, A. & Prestrud, P. (eds.), A Catalogue of Svalbard Plants, Fungi, Algae, and Cyanobacteria. *Norsk Polarinstitut Skrifter* 198: 9–55.

- Ertter, B. & Bowerman, M. L. 2002. The Flowering Plants and Ferns of Mount Diabolo, California. California Native Plant Society, Sacramento.
- Essl, F. & Rabitsch, W. (eds.). 2002. *Neobiota in Österreich*. Umweltbundesamt GmbH, Wien.
- Florence, J., Waldren, S. & Chepstow-Lusty, A. J. 1995. The flora of the Pitcairn Islands: a review. *Biol. J. Linn. Soc.* 56: 79–119.
- Frodin, D. G. 2001. Guide to Standard Floras of the World, ed. 2. Cambridge Univ. Press, Cambridge.
- **Fournet, J.** 2002. Flore Illustrée des Phanérogames de *Guadeloupe et de Martinique*. Cirad & Gondwana Editions, Tartane (Trinité, Martinique).
- Godwin, H. 1975. *The History of the British Flora*, ed. 2. Cambridge Univ. Press, Cambridge.
- Gojdicová, E., Cvachová, A. & Karasová, E. 2002. Zoznam nepôvodných, inváznych a expanzívnych cievnatých rastlín Slovenska 2. Ochrana Prírody 21: 39–58.
- **Goldblatt, P. & Manning, J.** 2000. Cape Plants—a conspectus of the Cape Flora of South Africa. *Strelitzia* 9: 1–743.
- Goodwin, B. J., McAllister, A. J. & Fahrig, J. 1999. Predicting invasiveness of plant species based on biological information. *Conserv. Biol.* 13: 422–426.
- Guerrant E. O. & Pavlik, B. M. 1998. Reintroduction of rare plants: genetics, demography, and the role of ex situ conservation methods. Pp. 80–108 in: Fiedler, P. L. & Kareiva, P. M. (eds.), *Conservation Biology for the Coming Decade*, ed. 2, Chapman & Hall, London.
- Gurevitch, J., Scheiner, S. M. & Fox, G. A. 2002. *The Ecology of Plants*. Sinauer, Sunderland.
- Hickman, J. C. (ed.). 1993. *The Jepson Manual*. Univ. California Press, Berkeley.
- Holub, J. & Jirásek, V. 1967. Zur Vereinheitlichung der Terminologie in der Phytogeographie. *Folia Geobot. Phytotax.* 2: 69–113.
- Hrusa, F., Ertter, B., Sanders, A., Leppig, G. & Dean, E. 2002. Catalogue of non-native vascular plants occuring spontaneously in California beyond those addressed in The Jepson Manual - Part I. *Madroño* 49: 61–98.
- Humphries, S. E., Groves, R. H. & Mitchell, D. S. 1991. Plant invasions of Australian ecosystems. *Kowari* 2: 1–134.
- **Jonsell, B.** (ed.). 2000. *Flora Nordica*, vol. 1. The Royal Swedish Academy of Sciences, Stockholm.
- Kloot, P. M. 1987. The naturalised flora of South Australia. 1. The documentation of its development. J. Adelaide Bot. Gardens 10: 81–90.
- Klotz, S., Kühn, I. & Durka, W. 2002. BIOLFLOR Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Bundesamt für Naturschutz, Bonn-Bad Godersberg.
- Kornas, J. 1990. Plant invasions in Central Europe: historical and ecological aspects. Pp. 19–36 in: di Castri, F., Hansen, A. J. & Debussche, M. (eds.), *Biological Invasions in Europe and Mediterranean Basin*. Kluwer Academic Publishers, Dordrecht.
- Kowarik, I. 2003. Biologische Invasionen: Neophyten und Neozoen in Mitteleuropa. Eugen Ulmer, Stuttgart.
- Kress, W. J., DeFilipps, R. A., Farr, E. & Daw Yin Yin Kyi.

- Lesica, P. 2002. *Flora of Glacier National Park*. Oregon State Univ. Press, Corvalis.
- Lohmeyer, W. & Sukopp, H. 1992. Agriophytes in der Vegetation Mitteleuropas. Schr. R. Vegetationskd. 25: 1–185.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80: 1522–1536.
- MacDonald, G. 2003. Biogeography: Introduction to Space, Time and Life. John Wiley & Sons, New York..
- Macpherson, P., Dickson, J. H., Ellis, R. G., Kent, D. H. & Stace, C. A. 1996. Plant status nomenclature. *Bot. Soc. British Isles News* 72: 13–16.
- Matthei, O. J. 1995. Manual de las Malezas que Crecen en Chile. Alfabeta Impresores, Santiago, Chile.
- McCauley, R. A. & Ballard, H. E. 2002. Inferring nativity and biogeographic affinities of central and marginal populations of *Froelichia floridana* (Amaranthaceae) from Inter-Simple Sequence Repeat (ISSR) markers. J. Torrey Bot. Club 129: 311–325.
- McNeely, J. A., Mooney, H. A., Neville, L. E., Schei, P. J. & Waage, J. K. (eds.). 2001. *Global Strategy on Invasive Alien Species*. IUCN, Gland.
- Mirkin, B. M. & Naumova, L. G. 1998. Nauka o Rastitelnosti. Gilem, Ufa.
- Mooney, H. A. 1999. A global strategy for dealing with alien invasive species. Pp. 407–418 in: Sandlund, O. T., Schei, P. J. & Viken, A. (eds.), *Invasive Species and Biodiversity Management*. Kluwer Academic Publishers, Dordrecht.
- Mooney, H. A. & Hobbs, R. J. 2000. Invasive Species in a Changing World. Island Press, Washington, D.C.
- Muhlenbach, V. 1979. Contributions to the synanthropic (adventive) flora of the railroads in St. Louis, Missouri, U.S.A. Ann. Missouri Bot. Garden 66: 1–108.
- Munz, P. A. 1968. A California Flora and Supplement. Univ. California Press, Berkeley.
- Neuffer, B. & Linde, M. 1999. Capsella bursa-pastoris: colonization and adaptation: a globe-trotter conquers the world. Pp. 49–72 in: van Raamsdonk, L. W. D. & den Nijs, J. M. C. (eds.), Plant Evolution in Man-made Habitats. Proceedings of the VIIth International IOPB Symposium. Hugo de Vries Laboratory, Amsterdam.
- **Oberdorfer, E.** 1994. *Pflanzensoziologische Exkursionsflora für Süddeutschland und die angrenzenden Gebiete*, ed. 7. E. Ulmer, Stuttgart.
- Palmer, M. W., Wade, G. L. & Neal, P. 1995. Standard for the writing of floras. *BioScience* 45: 339–345.
- Prach, K. & Wade, M. 1992. Population characteristics of expansive perennial herbs. *Preslia* 64: 45–51.
- Preston, C. D. 1986. An additional criterion for assessing native status. *Watsonia* 16: 83.
- Preston, C. D., Pearman, D. A. & Dines, T. D. 2002. New Atlas of the British and Irish flora. Oxford Univ. Press, Oxford.
- **Provost, M.** 1998. *Flore Vasculaire de Basse-Normandie*, vol. 2. Université de Caen, Caen.
- Pyšek, P. 1995. Recent trends in studies on plant invasions (1974–93). Pp. 223–236 in: Pyšek, P., Prach, K., Rejmánek, M. & Wade, M. (eds.), *Plant Invasions: General Aspects and Special Problems*. SPB Academic Publishing, Amsterdam.

- Pyšek, P. 1998. Is there a taxonomic pattern to plant invasions? Oikos 82: 282–294.
- **Pyšek, P.** 2003. How reliable are data on alien species in Flora Europaea? *Flora* 198: 499–507.
- Pyšek, P., Jarošík, V. & Kucera, T. 2002a. Patterns of invasion in temperate nature reserves. *Biol. Conserv.* 104: 13–24.
- Pyšek, P., Sádlo, J. & Mandák, B. 2002b. Catalogue of alien plants of the Czech Republic. *Preslia* 74: 97–186.
- Pyšek, P., Sádlo, J., Mandák, B. & Jarošík, V. 2003. Czech alien flora and a historical pattern of its formation: what came first to Central Europe? *Oecologia* 135: 122–130.
- Randall, J. M. 1997. Defining weeds of natural areas. Pp. 18–25 in: Luken, J. O. & Thieret, J. W. (eds.), Assessment and Management of Plant Invasions. Springer, New York.
- Randall, R. P. 2002. A Global Compendium of Weeds. R. G. & F. J. Richardson, Melbourne.
- Rejmánek, M. 1995. What makes a species invasive? Pp. 3–13 in: Pyšek, P., Prach, K., Rejmánek, M. & Wade, M. (eds.), *Plant Invasions: General Aspects and Special Problems.* SPB Academic Publishing, Amsterdam.
- Rejmánek, M. 1996. Species richness and resistance to invasions. Pp. 153–72 in: Orians, G. H., Dirzo, R. & Cushman, J. H. (eds.), *Diversity and Processes in Tropical Forest Ecosystems*. Springer Verlag, Berlin.
- Rejmánek, M. 2000. Invasive plants: approaches and predictions. Austral Ecol. 25: 497–506.
- Rejmánek, M. 2001. Cape Floristic Kingdom (review of Cape plants: a conspectus of the Cape flora of South Africa by P. Goldblatt & J. Manning, 2000). *Diversity Distrib.* 7: 303.
- Rejmánek, M., Richardson, D. M., Barbour, M. G., Crawley, M. J., Hrusa, G. F., Moyle, P. B., Randall, J. M., Simberloff, D. & Williamson, M. 2002. Biological invasions: politics and the discontinuity of ecological terminology. *Bull. Ecol. Soc. Amer.* 83: 131–133.
- Rejmánek, M., Richardson, D. M., Higgins, S. I., Pitcairn, M. & Grotkopp, E. In press. Invasive species: a new synthesis. In: Mooney, H. A., McNeeley, J. A., Neville, L., Schei, P. J. & Waage, J. (eds.), *Invasive Alien Species: Searching for Solutions*. Island Press, Washington, D.C.
- Rhoades, A. F. & Klein, W. M. 1993. The Vascular Flora of Pennsylvania. American Philosophical Society, Philadelphia.
- Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Panetta, F. D. & West, C. J. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity Distrib.* 6: 93–107.
- Robinson, G. R., Yurlina, M. E. & Handel, S. N. 1994. A century of change in the Staten Island flora: ecological correlates of species losses and invasions. *Bull. Torrey Bot. Club* 121: 119–129.
- Rothmaler, W., Jäger, E. J. & Werner, K. 2002. Exkursionsflora von Deutschland. Band 4. Gefäßpflanzen. Spektrum, Heidelberg.
- Ryves, T. B., Clement, E. J. & Foster, M. C. 1996. *Alien Grasses of the British Isles*. Botanical Society of the British Isles, London.
- Saltonstall, K. 2002. Cryptic invasion by non-native genotypes of the common reed, *Phragmites australis*, into North America. *Proc. Natl. Acad. Sci.*, U.S.A. 99: 2445–2449.

- Schroeder, F. G. 1969. Zur Klassifizierung der Anthropochoren. Vegetatio 16: 225–238.
- Smith, P. M. 1986. Native or introduced? Problems in the taxonomy and plant geography of some widely introduced annual brome-grasses. *Proc. Royal Soc. Edinburgh* 89B: 273–281.
- Space, J. C., Waterhouse, B. M., Miles, J. E., Tiobech, J. & Rengulbai, K. 2003. Report to the Republic of Palau on Invasive Plant Species of Environmental Concern. U.S.D.A. Forest Service, Pacific Southwest Research Station, Institute of Pacific Islands Forestry, Honolulu.
- Spencer, R. 1995–2002. Horticultural Flora of South-Eastern Australia, vol. 1–4. Univ. New South Wales Press, Sydney.
- Stace, C. 1991. New Flora of the British Isles. Cambridge Univ. Press, Cambridge.
- State of Washington Department of Natural Resources. 1982. Endangered, Threatened and Sensitive Vascular Plants of Washington. Department of Natural Resources, Washington.
- Stuckey, R. L. & Barkley, T. M. 1993. Weeds. Pp. 193–198 in: Flora of North America Editorial Committee (ed.), *Flora* of North America. Oxford Univ. Press, New York.
- Thellung, A. 1905. Einteilung der Ruderal- und Adventivflora in genetische Gruppen. In: Naegeli, O. & Thellung, A. (eds.), Die Flora des Kanton Zürich, 1. Teil. Die Ruderalund Adventivflora des Kanton Zürich. Vjschr. Naturforsch. Ges. Kanton Zürich 50: 232–236.
- Thellung, A. 1918–1919. Zur Terminologie der Adventiv- und Ruderalfloristik. *Allg. Bot. Zeitschr.* 24/25: 36–42.
- Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M. & Webb, D. A. (eds.). 1964–1980. *Flora Europaea*, vols. 1–5. Cambridge Univ. Press, Cambridge.
- Wacquant, J. P. 1990. Bigeographical and physiological aspects of the invasion by *Dittrichia* (ex-*Inula*) viscosa W. Greuter, a ruderal species in the Mediterranean Basin. Pp. 353–364 in: di Castri, F., Hansen, A. J. & Debussche, M. (eds.), *Biological Invasions in Europe and the Mediterranean Basin*. Kluwer Academic Publishers, Dordrecht.
- Waldren, S., Weisler, M. I., Hather, J. G. & Morrow, D. 1999. The non-native vascular plants of Henderson Island, South-Central Pacific Ocean. *Atoll Res. Bull.* 463: 1–14.
- Walters, S. M., Alexander, J. C. M., Brady, A., Brickell, C.D., Cullen, J., Green, P. S., Heywood, V. H., Matthews, V. A., Robson, N. K. B., Yeo, P. F. & Knees, S. G. (eds.). 1989. *The European Garden Flora. Vol. 3.* Dicotyledons (Part I). Cambridge Univ. Press, Cambridge.
- Walters, S. M., Brady, A., Brickell, C. D., Cullen, J., Green, P. S., Lewis, J., Matthews, V. A., Webb, D. A., Yeo, P. F. & Alexander, J. C. M. (eds.). 1984. The European Garden Flora. Vol. 1. Monocotyledons (Part 1). Cambridge Univ. Press, Cambridge.
- Walters, S. M., Brady, A., Brickell, C. D., Cullen, J., Green, P. S., Lewis, J., Mathews, V. A., Webb, D. A., Yeo, P. F. & Alexander, J. C. M. (eds). 1986. The European Garden Flora. Vol. 2. Monocotyledons (Part II). Cambridge Univ. Press, Cambridge.
- Washington Natural Heritage Program. 1984. Endangered, Threatened and Sensitive Vascular Plants of Washington. Washington Natural Heritage Program, Seatttle.

Washington Natural Heritage Program. 1997. Endangered,

Threatened and Sensitive Vascular Plants of Washington with Working List of Rare Non-vascular Species. Washington State Department of Natural Resources, Seattle.

- Webb, D. A. 1985. What are the criteria for presuming native status? *Watsonia* 15: 231–236.
- Weber, E. F. 1997. The alien flora of Europe: a taxonomic and biogeographic overview. J. Veget. Sci. 8: 565–572.
- Webster, L. 1992. Origin and distribution of adventive alien flowering plants in Hawai'i. Pp. 99–154 in: Stone, C. P., Smith, C. W. & Tunison, J. T. (eds.), Alien Plant Invasions in Native Ecosystems of Hawai'i: Management and Research. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu.
- Williamson, M. 1993. Invaders, weeds and the risk from genetically modified organisms. *Experientia* 49: 219–224.
- Williamson, M. 1996. *Biological Invasions*. Chapman & Hall, London.
- Williamson, M. 2002. Alien plants in the British Isles. Pp. 91–112 in: Pimentel, D. (ed.), Biological Invasions: Environmental and Economic Costs of Alien Plant, Animal and Microbe Species. CRC Press, Boca Raton.
- Wu, S.-H., Chaw, S. & Rejmánek, M. 2003. Naturalized Fabaceae (Leguminosae) species in Taiwan: the first approximation. *Bot. Bull. Acad. Sci. Sin.* 44: 59–66.
- **Zohary, M.** 1962. *Plant Life of Palestine, Israel and Jordan.* The Ronald Press, New York.