SPSD II

INVASIVE PLANTS IN BELGIUM: PATTERNS, PROCESSES AND MONITORING (INPLANBEL)

EV-27

SCIENTIFIC SUPPORT PLAN FOR A SUSTAINABLE DEVELOPMENT POLICY

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SCIENTIFIC SUPPORT PLAN FOR A SUSTAINABLE DEVELOPMENT POLICY
(SPSD II)

Part 2:
Global change, Ecosystems and Biodiversity

FINAL REPORT

INVASIVE PLANTS IN BELGIUM: PATTERNS, PROCESSES AND MONITORING
(INPLANBEL)

EV/27

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TABLE OF CONTENTS

ABSTRACT

The spread of invasive species into native ecosystems and habitats is known to be the second largest cause of current biodiversity loss worldwide, after habitat destruction. Yet the underlying mechanisms of invasive outbreaks are still poorly known. This hampers our understanding of the spatio-temporal patterns and ecosystem impacts associated to invasions, and precludes effective early identification of high-risk species. In many regions the past and current invaders have even never been surveyed. In the current project, invasive species match at least two criteria : 1) being an alien (species, subspecies or lower taxon, introduced outside its natural past or present distribution); 2) reproduce and increase its range in its new environment.

The project provided a multifunctional and multi-scale analysis of alien plant invasion in Belgium. The general aim was to provide a framework for the evaluation of the threat, for the development of policies and management strategy, and for the elaboration of further research programmes. The specific aims were

(1) to identify universally valid principles of biological invasion through a combined analysis of ecophysiological species and community traits, as a basis for pre-invasion risk assessment;

(2) to analysize the consequences of a set of invasive species on ecosystems properties;

(3) to provide a detailed analysis of the spreading of a set of invasive species at the landscape level, for a better understanding of the relation between invasion and human land use;

(4) to provide a synthesis on plant invasion in Belgium in the form of a structured list of exotic species and an evaluation of their success of invasion.

The results are discussed from a management point of view.

INTRODUCTION

1. Context and objectives

While anthropogenic global change has made some species decline, others have thrived and proliferated, sometimes with dramatic impacts on biodiversity. Such species are referred to as ‘invasive'. Most recent authoritative reviews defined an alien invasive species or taxon as (1) being an alien (species, subspecies or lower taxon, naturalized outside its natural past or present distribution), (2) reproducing and increasing its range in its new environment at a certain minimal speed (Richardson *et al.* 2000; Pyšek *et al.*, 2004). The introduction and spread of non-native species has become a global ecological and conservation problem as invasive organisms are increasingly altering terrestrial and aquatic communities worldwide (Parker *et al.*, 1999; Pimentel *et al.*, 2000; Byers *et al.*, 2002, Levine *et al.*, 2003; Gurevitch and Padilla, 2004).

In order to develop adequate knowledge to address this problem, it is important that nations undertake research on and monitoring of invasive alien species, including documentation of (1) the history and ecology of invasion (origin, pathways, process dynamics and impact of man), (2) the biological characteristics of the invasive alien species, invaded communities and landscapes, and (3) the associated impacts at the ecosystem, species and genetic level. So far, no clear scientific strategy had been developed in the context of the problem of invasive plant species in Belgium. This resulted in a lack of scientific basis on the aforementioned subjects necessary for building an early warning system and monitoring-management strategy of ongoing invasions.

The INPLANBEL project provided a multifunctional and multi-level analysis of alien plant invasion in Belgium. The general aim was to provide the basic framework for the evaluation of the threat, for the development of policies and management strategy and for the development of further research programs.

Specific aims of the project were:
- to provide a synthesis on plant invasion in Belgium and particularly to provide a structured list of exotic species with an evaluation of their success of invasion
- to identify universally valid principles of biological invasion through a combined analysis of species and community traits taking into account the ecophysiological traits as a basis for pre-invasion risk assessment
- to provide a detailed analysis of the spread of a sample of invasive species at the landscape level, especially species with potential environmental impact, for a better understanding of the relation between invasion and human land use
- to provide an analysis of the consequences of a set of invasive species on ecosystems

2. Scientific strategy

2.1 Overall strategy

The INPLANBEL project proposed an integrated research approach that examined both the causes and the processes of invasion at local (site), landscape and regional (Belgium) scale. At each scale, the project focused on the particular process(es) that was (were) expected of being the most relevant (Figure 1). Because of the various natures of processes examined, each partner of the project was responsible for a particular type of analysis in relation to its own area of expertise: ecophysiology, soil and mineral nutrition ecology, dispersal and landscape ecology, taxonomy and biogeography.

Scale	Invasion Process	Tasks in INPLANBEL
	Introduction	
Site	*Initial colonisation* *Installation*	Analysis of species and community traits that promote invasive success Analysis of the consequences of invasion on ecosystem properties
Landscape	*Propagule Dispersal* *Metapopulation dynamics*	Analysis of interactions between species dispersal capacities and landscape structure
Geographical region	*Invasion*	Set up of check list of exotic taxa in Belgium with an estimation of their invasive success Analysis of the pattern of spreading of a selected set of species

***Figure 1**- Tasks of the INPLANBEL project in relation to scale of organisation and invasion steps*

The corner piece of the integrative nature of the project was the fact that all the partners worked on a common set of species recognized as problematic invaders in Belgium (and more generally in Western Europe). In the same way, the partners worked on common study sites whenever relevant. Promoting a collaborative study of the different processes of invasion on a same set of species was expected to significantly increase our understanding of invasion for those species as well as our understanding of interactions between the different scales at which the process of invasion occurs.

The selected species for common analysis fulfilled the following criteria: (1)

occurring with large and well established populations in a large area in Belgium for the analysis of ecosystem properties modification; (2) being invaders of habitats of high conservation value (based on advice from nature reserve managers a preliminary survey among representatives of RNOB nature reserves); (3) being invasive in contrasting types of habitats. The following species were selected: *Prunus serotina, Senecio inaequidens, Polemonium caeruleum, Heracleum mantegazzianum, Solidago gigantea, Fallopia japonica, Rosa rugosa*, *Impatiens glandulifera, Impatiens parviflora.* From those species, five were effectively included in all analyses: *Senecio inaequidens, Heracleum mantegazzianum, Solidago gigantea, Fallopia japonica, Impatiens glandulifera.* The other ones were used only for more specific tasks of the project. Additional species were considered for the trait analysis, these are exotic species that were recorded on the Belgian territory but have failed to become invasive and are considered as pest species. Tropical C_4 grasses were also considered for a specific task in the landscape analysis.

2.2 Site x species : predicting invasion success.

As increasing numbers of alien species spread around the globe, prediction systems that identify the (few) future invaders among those exotics are urgently needed, but only a handful of attempts have been successful so far. However, numerous studies have tried to elucidate the mechanisms controlling successful invasion. Some deem traits of the invasive species are the driving forces (invasiveness; Maillet & Lopez-Garcia, 2000; Kolar & Lodge, 2001; Lake & Leishman, 2004), others point at the susceptibility of ecosystems to invasion (invasibility; Lonsdale, 1999; Davis et al., 2000; Smith & Knapp, 2001). These one-sided approaches in fact mutually exclude each other: explaining invasive success only via plant traits assumes that a species can be invasive anywhere as soon as it possesses those traits, regardless of the invaded system (in other words: invaded-system traits are irrelevant). Conversely, the use of ecosystem traits alone implicitly assumes that every alien plant species can invade an ecosystem typified by such traits, in other words: invader traits do not matter. Observations clearly do not support this. Together with other authors (Manchester & Bullock, 2000; Milbau et al., 2003), we plead for combining both approaches, and the current study proposes an analysis of invasion success both from invader and invasible-system characteristics.

Ideally, a successful invasion requires the invader to complete a number of consecutive steps: (1) invader seeds have to germinate in sufficient proportion, (2) seedlings have to survive, (3) developing invader plants have to withstand the competition from neighbours and (4) produce viable seeds, which (5) need to be efficiently dispersed. In each of theses stages, lack of success can slow down the invasion process. The current study focuses on the third and fourth step by measuring height, biomass and seed production of invaders as success measures, from the perspective that large invaders can acquire more of the available resources and better suppress native competitors. Beside successful propagation and establishment, we also studied invaders from the perspective of impact, or harmfulness. Different plant and ecosystem traits may explain success and impact, and different predictive strategies may therefore be required (Nijs *et al.*, 2004).

A central tenet to our approach is that a native species is not the counterpart of an invasive species. For example, based upon 79 native-invasive comparisons, Daehler (2003) concluded that both groups did not differ significantly in performance (biomass). Natives may be invasive elsewhere (Rejmánek, 2000), and successful invasive and successful native species may be more alike than successful and unsuccessful invasive species (Davis et al., 2000). Moreover, differences between aliens and non-aliens may be confounded with differences between species originating from different parts of the world. By setting natives against invaders, promising predictors may therefore get lost, because they could be shared by both groups. For this reason, the current study includes only alien species, in an attempt to explain the variation in their growth and seed production.

By studying the growth, biomass, seed production and impact of 11 alien species in three unmanipulated field sites each (including nature reserves), and measuring 28 invader traits and 18 invasible system traits in each species × site combination, we address the following questions: (1) Which plant traits are predictors of invasiveness or impact across sites?, (2) Which ecosystem traits are predictors of invasibility or impact across invader species?, (3) Do combinations of plant and ecosystem traits enhance the predictability of invasive success (growth and seed production) relative to using only plant or only ecosystem traits? Which combinations maximize the explained variance of success?

2.3 Site x species : consequences of invasion

Exotic plant invasions often have dramatic impacts on the resident vegetation by modifying its composition and structure (Levine *et al.* 2003). Most of the time, the driving force of this direct impact is competition for resources (light, water, nutrients). The more subtle impacts of plant invasions on ecosystem functioning are comparatively less studied. Two important factors controlling ecosystem functioning are soil properties and nutrient fluxes between plant and soil. The recent review of Ehrenfeld (2003) concluded that invasive species most often increased productivity of invaded ecosystems. They also enhance N availability due to a more easily decomposable litter compared to the resident vegetation. Compared to C and N, the impacts of invasions on base cations and phosphorus availability have been rarely assessed. From the scarce data available, it appears that increased nutrient availability has been more often observed than decreased availability (Musil 1993;

Scott *et al.* 2001; Vanderhoeven *et al.* 2005; Chapuis-Lardy *et al.* in press but see Belnap & Philips 2001; Leary *et al.* 2006). However, most published studies consider the impacts of one species at one particular site. Their results are thus difficult to generalise since one species can have contrasting impacts depending on site (Belnap & Philips 2001; Scott *et al.* 2001).

We selected 9 of the most successful alien plant species in various terrestrial ecosystems. These species belong to different functional groups: two annual species (*Impatiens glandulifera, I. parviflora*), three hemicryptophytes (*Senecio inaequidens, Heracleum mantegazzianum, Polemonium caeruleum*), two perennial rhizomatous geophytes (*Solidago gigantea, Fallopia gigantea*), a woody shrub (*Rosa rugosa*) and a tree (*Prunus serotina*).

In this report, we examine the impacts of those 9 species on soil chemical properties, aboveground primary productivity and nutrient stocks in standing biomass by comparing invaded and adjacent uninvaded plots as proposed by Walker and Smith (1996). The questions addressed are: (1) What is the magnitude and direction of the impacts of alien invasive species on soil properties ? (2) Do impacts vary depending on element, species and site? (3) Are impacts on soil explained by differences in nutrient use between native and alien species (=altered biomass production or nutrient concentration in biomass)?

2.4 Landscape x species : patterns of spreading at the landscape level.

Besides generalization based on traits, detailed studies on the population biology of invasive species in a spatially explicit context are needed to fully understand the mechanisms of ongoing invasions. The process of invasion has two distinct components: increase in population size (demographic rates) and increase in area (dispersal of propagules). The particularity of invaders is the fact that immigration, and not the usually overriding balance between births and deaths, plays a major role in determining abundance (Hengeveld, 1989). Hence, dispersal analysis is a key feature in understanding the success of invasive species. Although much has been written on the dispersal capacities of invaders, the number of detailed studies of dispersal ability and realized dispersal patterns is surprisingly low (see Lonsdale, 1993; Higgins *et al.*, 2001). From a community perspective, the studies of characteristics of habitats (community traits) is not sufficient to understand dispersal process and spreading patterns, because realized dispersal is highly dependent on landscape structure (presence of corridors of migration, density and spatial arrangement of favourable habitats, presence of physical barriers, …). Assessing the behaviour of invasive species at the landscape scale is particularly important also from a management perspective because political decisions concerning management strategy will generally concern large geographic areas (Higgins *et al.*, 2000). To better document patterns and process of invasion at the landscape scale, two complementary specific study cases were explored. First, a study of habitat selection and dispersal of the aforementioned common sample of exotic species in ecological landscape units has been performed in order to define the habitats colonized by the species and to analyze the spatial distribution of the species in relation to the structure of the landscape (assessed with the matrix-patch-corridor theory and human land-use) and their dispersal capacities. Second, a more specific analysis was conducted on C_4 grasses of tropical origin which occur as weeds of maize fields. For these species, a study of metapopulation dynamics has been undertaken at three spatial scales. As this approach was more focused on agricultural land use, it complemented the first task wherein selected species were not linked to agricultural activities.

In the past decades maize has become a much more important crop in western European agriculture. A number of characteristics of this crop, including its links with worldwide economic and transportation networks, limited crop rotation, and the role played by agricultural contractors, make the relatively new maize field habitat vulnerable for colonization by new alien weeds. In Belgium, a number of alien C_4 grasses, together with indigenous and/or since long naturalized species, have recently expanded considerably in and along maize fields. They therefore offer opportunities for case studies of the dynamics of introduction, dispersal, and population fluctuations of aliens. Our primarily descriptive research was carried out on three different levels: (1) mapping the distribution of all C_4 grasses in a 16 x 20 km area between Bruges and Ghent, based on 1 km² units; (2) mapping the distribution of populations of two species in a more limited area (for *Setaria faberi* circa 12 km², for *Digitaria aequiglumis* slightly less than 1 km²), with a two year follow up of their fluctuations; and (3) the description and 3 year monitoring of the presence of C_4 grasses in a number of transects (25 m long) along maize fields.

2.5 Region x species (flora) : Catalogue of neophytes in Belgium (1800-2005) and Invasion histories.

The presence of alien species in local floras is obviously linked to various kinds of human activities and this relation is as old as human activity itself. Parallel to the increase of the velocity and volume of intercontinental trade it has become clear that the number of arrivals of ‘new’ species has never been as high as during the last decades (see this report for the Belgian situation). On the other hand, those species have never received more attention than nowadays. Specialized researchers continuously pay attention to sites with high potential for the arrival of new aliens. To some degree, the proliferation of aliens and the follow up of their invasion processes are explained by a changed perception of this group of plants. Besides the ‘traditional’ attention for disappearing and regressing species, modern botanists are as much, if not more, interested in and involved with new and progressing ones (Vanhecke & Hoste 2006).

Most of the new arrivals are harmless and disappear after a short stay: their ecological demands do not sufficiently fit the available resource or climatic niches in the local habitat. During the last decades, it became more and more obvious that worldwide, the unwanted and accelerating intercontinental exchange of flora-elements causes problems by suppressing and endangering native floras to a degree that the damage becomes economically measurable. Since then, invading plants, that might be pest plants here and innocent weeds elsewhere or vice versa, have become an economic and conservation problem and as such they function as an important new drive in the organization of scientific research.

A major item was the establishment of a catalogue of all neophyte vascular plants observed in Belgium during the whole of the ±150 years long period of botanical observations (1850-present). This national catalogue can be seen as an extension and a completion of the catalogue made for the species that naturalized in Flanders after 1972 (Verloove 2002). This catalogue creates the possibility to measure the extent of the invasive plants problem for the first time in Belgium in an objective way. A comprehensive list of alien species with floristic status, degree of naturalization, date and mode of introduction, … is indeed an essential tool for the study of plant invasions. Through INPLANBEL this gap has now been filled.

Although experienced field botanists can often see it happen in real time, the comparison of successive distribution maps covering a certain period remains a necessary step to decide whether or not a species is on the move. By measuring differences in frequency and occupied area between periods, distribution maps permit to quantify the magnitude of the expansion or regression of taxa. The accuracy of these estimates is bound by the quality of the compared distribution maps that are based on heterogeneous collections of all kinds of floristic data, gathered by many persons, in different periods and under contrasting circumstances. Even when those data are collected on purpose and systematically, flora mapping remains an activity determined amongst others by the incidental meetings between persons and plants. It is a major characteristic of our approach that we try to calibrate the original observations by this circumstantial data behind the ‘raw’ floristic data and that we construct different frames according to the main characteristics and shortcomings of the different types of data (and periods).

3. Organization of the report

Because each of the project aims listed under ‘*Context and Objectives’* required a specific scientific approach, we present the detailed methodology, results and discussions separately in four main sections:

Section 1: Explaining invasive success: trait analysis of species and communities
Section 2: Impact of plant invasions on ecosystem properties
Section 3: Patterns and processes of invasion at the landscape scale.
Section 4: A structured check list of alien species in Belgium and invasion histories.

The general discussion provides both a synthesis of the main conclusions of each section and a discussion of the importance of these conclusions for invader management

SECTION 1: EXPLAINING INVASIVE SUCCESS: TRAIT ANALYSIS OF SPECIES AND COMMUNITIES

1. Materials and Methods

1.1 Design

Eleven species, exotic to Belgium and covering a range of invasive success, were selected based on expert knowledge: *Cerastium tomentosum* , *Fallopia japonica*, *Heracleum mantegazzianum*, *Impatiens glandulifera*, *Impatiens parviflora*, *Lathyrus latifolius*, *Prunus serotina*, *Rosa rugosa*, *Senecio inaequidens*, *Solidago gigantea* and *Xanthium orientale* (Verloove, 2002). These species were studied in 33 sites (three per species) across North Belgium, 13 of which were situated in nature reserves. Divergent sites per species (e.g. woodland, grassland, roadside verges) were chosen to have a wide range in invasible-system traits, as opposed to the wide range in species traits expected from selecting 11 invaders characterized by varying success. At each site we quantified (i) traits of the invasive species, (ii) traits of the invasible ecosystem and (iii) realized growth and fitness of the invaders, expressed as invader height, invader aboveground biomass or invader seed production. Impact measures were provided by the ULB. Plant and ecosystem traits were then linked to invader growth or seed production via regression analysis, which we hypothesize to be maximized when traits conferring invasiveness and traits conferring invasibility co-occur. A first series of traits (“seasonal traits”) was sampled both in spring (26 May - 27 June 2003) and in summer (21 July - 7 August 2003). We included two seasons (i) because traits of influence only in one season could otherwise remain undetected, (ii) to determine the best season for prediction, and (iii) to evaluate the seasonal variability of the traits. A second series of traits, less subject to seasonal influences (“annual traits”), was sampled once-only on - for each trait - relevant points in time.

1.2 Measurements

Traits of invasive species

Isolated invader plants were selected that had not (yet) formed monoculture invader stands, as this might change their traits. Furthermore it is the traits of isolated invaders that determine the interaction with natives, which in turn determines invasiveness. For each species at each site, we measured the following 28 plant traits:

(i) The seasonal traits (determined both in spring and summer) included photosynthetic variables determined on the youngest fully expanded leaves (YFEL) of four replicate plants: light-saturated photosynthetic rate (Pmax, µmol CO2 m-2 s-1), dark respiration rate (Rd, µmol CO2 m-2 s-1), light compensation point (Ic, µmol photons m-2 s-1) and apparent quantum efficiency (α, µmol CO2 µmol photons–1).

These variables were derived from CO2 exchange rates at four light intensities: 1800 or 1200 (the latter for shaded invaders), 100, 50 and 0 µmol photons m-2 s-1, measured with a LI-6400 gas exchange system (LI-COR, Inc., Lincoln, NE, USA) equipped with a 6400-02B LED light source. Sampling was done at ambient humidity between 20 and 25° C at decreasing light intensity on the same leaf, allowing minimum 4 min stabilization. The reported Pmax and Rd values are the measured rates at 1800 (1200) and 0 µmol photons m-2 s-1, respectively, and α and Ic the calculated slope and X-intercept of the straight line connecting the values at 0 and 50 µmol photons m-2 s-1.

(ii) A second group of seasonal plant traits concerned morphological and chemical leaf attributes. The leaf part used to determine CO2 exchange rate was excised to measure the area (LAleaf, cm2), then dried (75° C, 24 h), weighed (Bleaf, g) and analyzed for carbon and nitrogen concentration on a mass basis (CYFEL, NYFEL, g kg-1) with a dry combustion C/N analyzer (NC-2100, Carlo Erba Instruments, Milan, Italy). Specific leaf area (SLA, cm2 g-1) was calculated as LAleaf×Bleaf-1, C:NYFEL (g g-1) as CYFEL×NYFEL-1, leaf nitrogen concentration on an area basis (NYFEL, area, g m-2) as NYFEL×SLA-1×104 and instantaneous photosynthetic nitrogen use efficiency (PNUE, µmol CO2 mol N-1 s-1) as Pmax×NYFEL, area-1×MN-1 with MN atomic mass of nitrogen.

(iii) A third series of seasonal traits (determined both in spring and summer) concerns size-related traits. Five randomly chosen, solitary plants were harvested above and belowground and dried (75° C, 24 h), after measuring their height ($H_{invader}$, cm). Subsequently, each plant was divided into roots, leaf blades, and other aboveground material to calculate shoot ($B_{invader}$) and total biomass, root: shoot ratio and leaf mass ratio (LMR).

(iv) To determine the annual plant traits, a separate series of YFEL (10 replicates, each on a different plant) was harvested at the beginning of the growing season (May-June, depending on species), dried (75° C, 24 h), and analyzed for Ca, Cu, Fe, K, Mg, Mn, P and Zn (ICP-AES, ElementYFEL, g kg-1). This procedure, supplemented with C and N analyses (NC-2100), was repeated at the end of the growing season (August-November, depending on species), to determine the element concentrations of the lowermost senescent leaves (Elementsenescent, g kg-1), selecting plants with about 50% senescent leaves. A resorption efficiency index (Relement) was calculated for each element as Elementsenescent×ElementYFEL-1, with low values indicating efficient resorption. To calculate Csenescent×CYFEL-1, and Nsenescent×NYFEL-1, we used the spring values of CYFEL and NYFEL, that were determined on the leaf parts used for the gas exchange measurements.

(v) The last annual plant trait was seed mass, calculated from 100 ripe and air-dry (20° C, 1 week) seeds, originating from 10 plants.

Traits of invasible ecosystems

To identify traits of ecosystems susceptible to invasion, in other words traits conferring invasibility, measurements were taken in uninvaded plots (but close to the invader population), to avoid collecting characteristics already modified by the invader. For each species at each site, we measured the following 18 ecosystem traits:

(i) Microclimate conditions were sampled as seasonal traits (spring and summer) at five replicate locations at ground level (so as experienced by invader seedlings) and at the top of the canopy, to quantify how they were modified by the vegetation. Air temperature (T, °C) and relative humidity (RH) were measured with a Kestrel 3000 Pocket Weather Meter (Nielsen-Kellerman, Boothwyn, PA, USA), yielding difference in temperature (ΔT), in vapor pressure (Δe, Pa) and in vapor pressure deficit (ΔVPD, Pa) above and below the canopy. Photon flux density of photosynthetically active radiation and red:far red ratio were determined with a JYP 1000 gallium arsenide quantum sensor (SDEC, Reignac sur Indre, France) and a Red/Far Red SKR 110 sensor (Skye Instruments Ltd, Powys, UK), respectively, yielding PAR penetration (PAR ratio, ground level/top of canopy) and RFR change (RFR ratio, ground level/top of canopy). Due to instrument failure, RFR ratios could not be measured in summer.

(ii) Community biomass (Bcommunity, kg m-2) was collected as an annual trait (July-August) according to the aboveground peak live standing crop method: standing biomass was cut off in six 1-m2 plots, dried (75° C, 24 h), weighed and ground. Element concentrations in the harvested material (Elementcommunity, g kg-1) were assessed by ICP-AES (Ca, Cu, Fe, K, Mg, Mn, P and Zn) or with the NC-2100 analyzer (C, N).

(iii) The cover of the uninvaded vegetation was estimated as an annual trait (July-August) using the Braun-Blanquet scale, converted into a linear scale (%). 1-m2 plots were selected until no more new species were recorded, yielding the total species richness of the site. Species diversity and evenness index (Shannon) were calculated for each plot category and N number of species, yielding an average H for the site.

(iv) A third group of annual traits comprised soil traits (see partim ULB). The following parameters were assessed: soil pH (pHH2O and pHKCl), trace elements, total C and N (Ctot, soil, Ntot, soil, g kg-1), CaCO3-carbon content (Ccarbo, soil), organic C content (Corg, soil) and C:Nsoil (calculated as Corg, soil×Ntot, soil-1).

Invasive success

Two measures of invader growth, aboveground biomass ($B_{invader}$) and height ($H_{invader}$) were measured in the spring and summer periods. Percentage of reproducing plants was estimated from 100 plants. For ten reproducing plants, all seeds were counted. Average individual seed production (number) was calculated as the product of both.

Impact

Impact measures: see partim ‘Section2’. Both differences and ratios of soil and vegetation characteristics of invaded and uninvaded plots were used.

1.3 Statistical analyses

Two data sets were used for growth. The spring data set consisted of all the seasonal traits and success measures determined in spring. This data set was supplemented with two types of annual traits: (i) the diversity-related variables, because stand diversity might also influence invader growth in spring, and (ii) ElementYFEL, measured at the beginning of the growing season. Relement, Bcommunity and Elementcommunity were not included as they are not necessarily representative of spring. The summer data set consisted of all seasonal traits and success measures determined in summer, in addition to all the annual traits since these might relate to invader growth in summer. The success measures were regressed on the traits after log10-transformation to improve normality of the residuals. Simple regressions were performed for each of the traits separately, and multiple regressions for each combination of a plant and an ecosystem trait, excluding cases “listwise” (a site was excluded from analysis if it had a missing value for one of the two independent variables). Multiple regressions were checked for multicollinearity using the variance inflation factor (VIF < 10).

Due to the large number of impacts (80) and traits (>100), screening for traits (both spring and summer data) explaining impact was performed by correlation analysis.

2. Results

2.1 Regression analyses

We first regressed $H_{invader}$, $B_{invader}$ and seed production on one plant or ecosystem trait at the time. To increase predictive power, we next performed multiple regressions on every possible combination of one plant and one ecosystem trait within the same data set (spring or summer). To reduce the risk of false positives associated with a large number of regressions, we evaluated the results for consistency between (i) spring and summer, (ii) $H_{invader}$ and $B_{invader}$, (iii) simple and multiple regressions, and (iv) multiple regressions with one composing trait in common. For impact measures, correlation analyses were performed.

$H_{invader}$ in spring

Six simple regressions were significant (nature of the relationship between brackets): $H_{invader}$ as a function of plant traits CYFEL (+) and MnYFEL (-), and as a function of ecosystem traits ΔT (-), ΔVPD (-), PAR ratio (-) and RFR ratio (-) (Figure 2). The ecosystem traits explained $H_{invader}$ to a greater extent, up to a maximum of 43.2%. The results suggest that fast-growing individual invaders have high carbon and low manganese concentrations in young leaves and occur preferentially in vegetation that greatly reduces temperature and light, and increases humidity, relative to the top of the canopy. Neither SLA, the photosynthetic variables, nor the diversity-related traits had explanatory power.

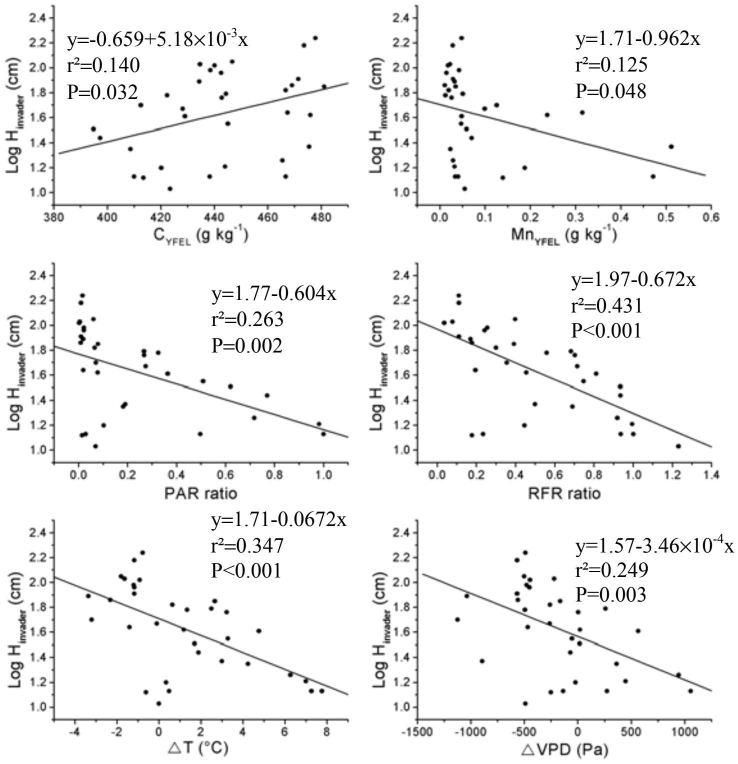


***Figure 2** - Significant simple regressions of invader height measured in spring on plant or ecosystem traits. Each symbol represents one species × site combination. C_{YFEL} and Mn_{YFEL}: carbon and manganese concentration in youngest fully expanded leaves; PAR or RFR ratio: ratio of photosynthetically active radiation or red:far red ratio at ground level to top of the canopy; ΔT and ΔVPD: difference in temperature and vapor pressure deficit between ground level and top of the canopy.*

The number of significant multiple regressions was much higher (data not shown) and the following combinations yielded the five highest r^2 values:

$H_{invader}$=2.24-5.42×10^{-4}SLA-0.840RFR ratio (r^2=0.708, p<0.001)
$H_{invader}$=2.10-1.25×$10^{-3}$$Mn_{YFEL}$-0.728RFR ratio ($r^2$=0.642, p<0.001)
$H_{invader}$=1.89-4.89×10^{-4}SLA-0.0822ΔT (r^2=0.576, p<0.001)
$H_{invader}$=1.75-0.822$N_{YFEL, area}$-0.214RFR ratio (r^2=0.549, p<0.001)
$H_{invader}$=1.80-0.117R_d-0.683RFR ratio (r^2=0.521, p<0.001).

These r^2 values were significantly greater than those of the best simple regressions on the composing variables (F-test, p<0.05). Whereas SLA, $N_{YFEL, area}$ and R_d themselves had no predictive power, they alien invasive species the predictive power of RFR ratio and ΔT. In the multiple regressions, the four microclimate traits determined all but two significant models, regardless of the combining plant trait. In contrast, only one of the 54 combinations with a diversity-related ecosystem trait explained $H_{invader}$.

$H_{invader}$ in summer

Six simple regressions were significant: $H_{invader}$ as a function of plant traits C_{YFEL} (+) and Mn_{YFEL} (-), and as a function of ecosystem traits ΔT (-), PAR ratio (-), $B_{community}$ (+) and $K_{community}$ (+) (Figure 3). As in spring, the ecosystem traits explained $H_{invader}$ better than the plant traits, up to a maximum of 54.8%. High YFEL carbon concentrations, low YFEL manganese concentrations, reduced temperature, and low light penetration contributing to invader growth, were patterns also found in spring, which makes it unlikely they were false positives. The positive relationships between $H_{invader}$ and $K_{community}$ and $B_{community}$ imply that invaders grow taller (and/or that tall invaders grow preferentially) in productive ecosystems.

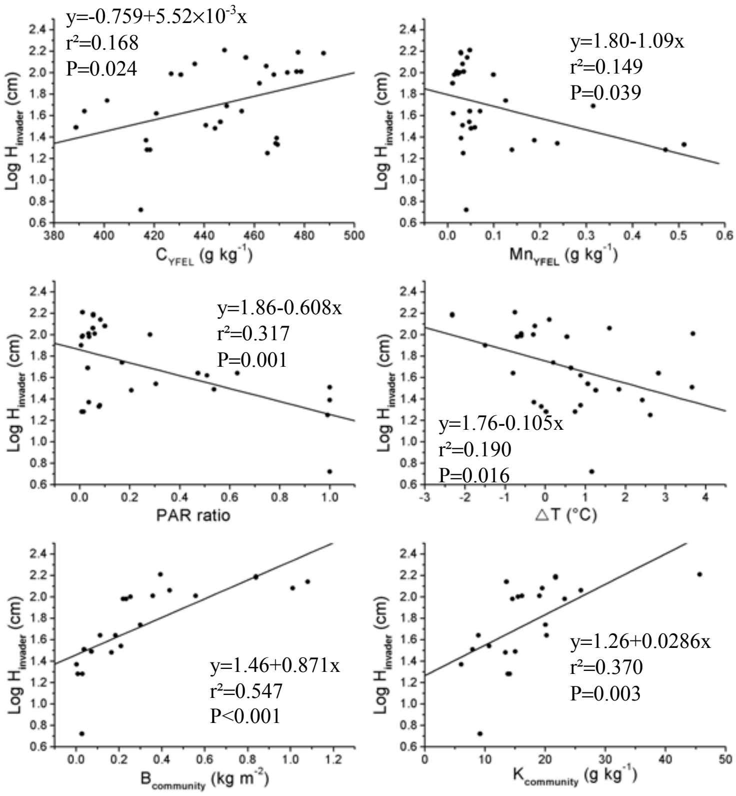


Figure 3 - *Significant simple regressions of invader height measured in summer on plant or ecosystem traits. Each symbol represents one species × site combination.* C_{YFEL} *and* Mn_{YFEL}*: carbon and manganese concentration in youngest fully expanded leaves; PAR ratio: ratio of photosynthetically active radiation at ground level to top of the canopy;* ΔT*: difference in temperature between ground level and top of the canopy;* $B_{community}$*: aboveground biomass of uninvaded vegetation;* $K_{community}$*: K concentration in uninvaded vegetation.*

Also in this season, the number of significant multiple regressions was much greater (data not shown) and the following combinations yielded the five highest r^2 values:

$H_{invader}=1.35+0.0534R_{Mn}+0.947B_{community}$ ($r^2=0.801$, $p<0.001$)

$H_{invader}=1.45+1.18\times10^{-3}R_{P}+0.973B_{community}$ ($r^2=0.789$, $p<0.001$)

$H_{invader}=1.39+0.0570R_{Mg}+0.970B_{community}$ ($r^2=0.735$, $p<0.001$)

$H_{invader}=2.44+1.26\times10^{-5}R_{K}+1.01B_{community}$ ($r^2=0.723$, $p<0.001$)

$H_{invader}=1.54-0.0430R_{Zn}+0.973B_{community}$ ($r^2=0.720$, $p<0.001$).

Again, these r^2 values were significantly greater than those of the best simple regressions on the composing variables (F-test, $p<0.05$). Most combinations with C_{YFEL} were significant (confirming its effect in spring), yet C_{YFEL} did not appear in the best five models. And, vice versa, though none of the nutrient resorption efficiencies were significant in the simple regressions, they were part of all of the best five models. Surprisingly, tall invaders had inefficient resorption (high values of the ratios) of Mn, P, Mg and K (not Zn). Similar to in spring, the diversity-related variables did not explain $H_{invader}$. All multiple regressions that included $B_{community}$ or $K_{community}$ were significant. In general, the regressions of $H_{invader}$ yielded similar r^2 values in spring and in summer when the same traits were used and a similar pattern arose of ecosystem traits driving $H_{invader}$ in the two seasons, except for the limited importance of ΔVPD in summer.

$B_{invader}$ in spring

Four simple regressions were significant: $B_{invader}$ as a function of plant traits C_{YFEL} (+), Mn_{YFEL} (-), α (+) and SLA (-) (Figure 4), but they explained little of $B_{invader}$ (maximum 33.7%). Surprisingly, none of the regressions on ecosystem traits were significant, whereas $H_{invader}$ had four microclimate predictors in spring and two in summer. The results suggest productive invasive plants are characterized by YFEL with high carbon and low manganese concentrations, high α and low SLA.

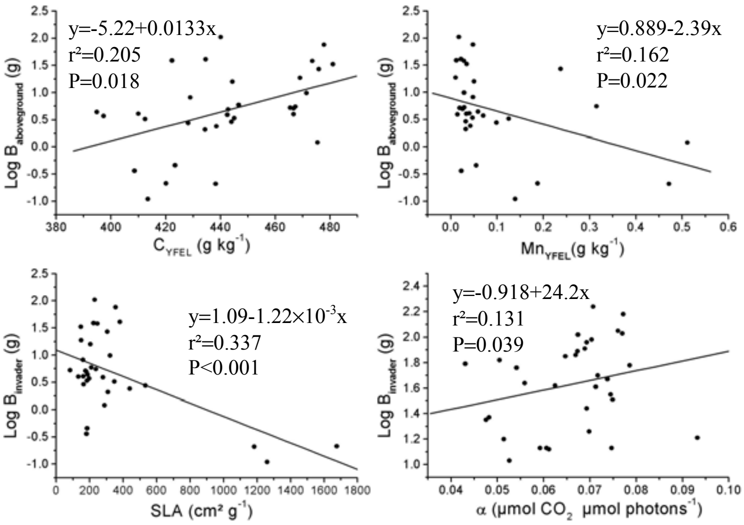


Figure 4 *- Significant simple regressions of invader aboveground biomass measured in spring on plant traits (no significant ecosystem traits). Each symbol represents one species × site combination. C_{YFEL} and Mn_{YFEL}: carbon and manganese concentration in youngest fully expanded leaves; SLA: specific leaf area; α: apparent quantum efficiency.*

Significant multiple regressions were again more numerous (data not shown), with the following combinations yielding the five highest r^2 values:

$B_{invader}$=1.73-1.52×10^{-3}SLA-1.06RFR ratio (r^2=0.554, p<0.001)
$B_{invader}$=1.22-1.37×10^{-3}SLA-6.68×$10^{-3}\Delta$T (r^2=0.408, p<0.001)
$B_{invader}$=1.30-1.38×10^{-3}SLA-0.659PAR ratio (r^2=0.400, p<0.001)
$B_{invader}$=1.35-1.36×10^{-3}SLA-72.9Δe (r^2=0.377, p=0.001)
$B_{invader}$=1.06-1.25×10^{-3}SLA-2.08×$10^{-4}\Delta$VPD (r^2=0.357, p=0.001).

Only the first model had a significantly greater r^2 than the corresponding simple regressions (F-test, p<0.05), therefore we heeded the remaining models no further.

$B_{invader}$ in summer

Thirteen simple regressions were significant: $B_{invader}$ as a function of plant traits $N_{YFEL, area}$ (+), C_{YFEL} (+), Mn_{YFEL} (-), SLA (-), R_d (-), I_c (+), α (+) and as a function of ecosystem traits $B_{community}$ (+), $K_{community}$ (+), $P_{community}$ (+), $Mn_{community}$ (-) and $Ca_{community}$ (+) (Figure 5). Contrary to the three previous analyses, neither plant nor ecosystem traits consistently had higher r^2 values, which ranged from 13.3% to 48.3%. $B_{invader}$ in summer shares C_{YFEL} and Mn_{YFEL} with the other three cases, α and SLA with $B_{invader}$ in spring, and $B_{community}$ and $K_{community}$ with $H_{invader}$ in summer. Again the role of manganese is striking: Mn_{YFEL} as well as $Mn_{community}$ were negatively linked to $B_{invader}$.

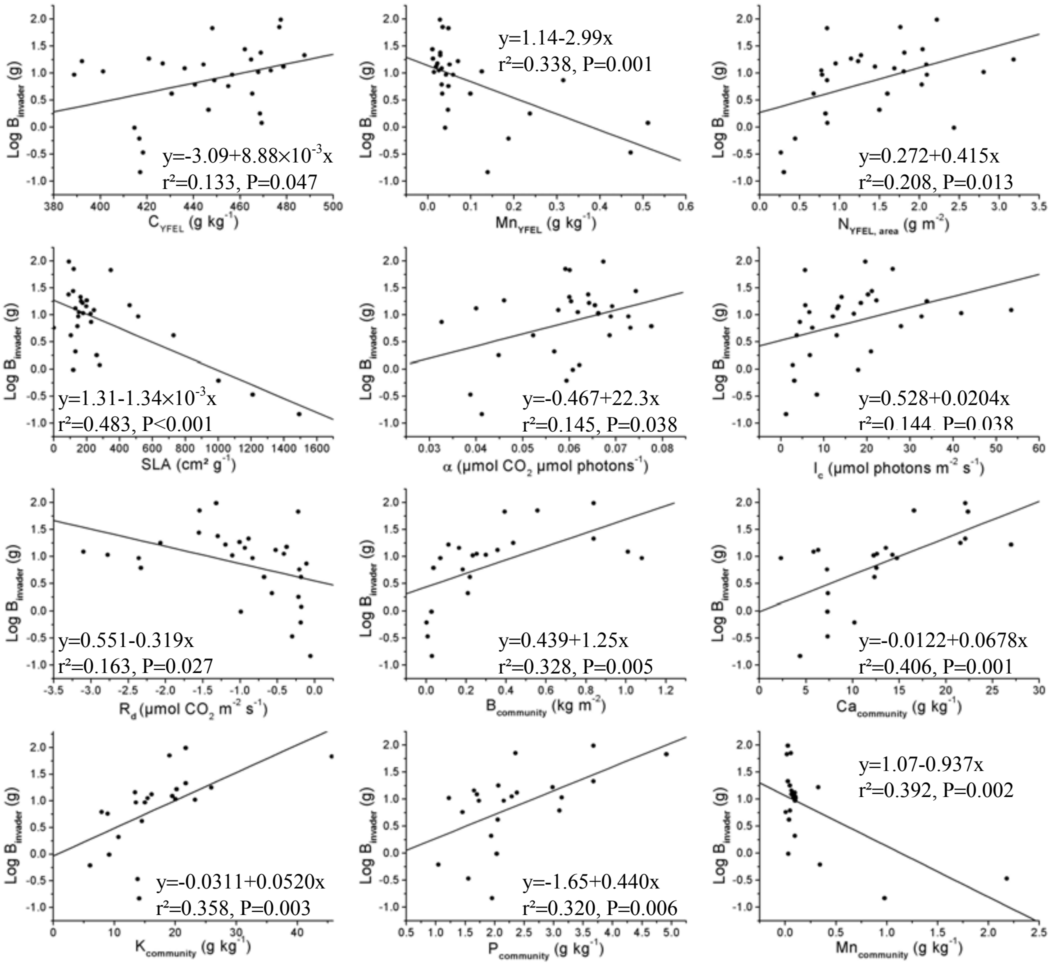


***Figure 5** - Significant simple regressions of invader aboveground biomass measured in summer on plant or ecosystem traits. Each symbol represents one species × site combination. C_{YFEL}, Mn_{YFEL} and $N_{YFEL, area}$: carbon, manganese and nitrogen concentrations in youngest fully expanded leaves; SLA: specific leaf area; R_d, I_c and α: dark respiration rate, light compensation point and apparent quantum efficiency of photosynthesis; $B_{community}$: aboveground biomass of uninvaded vegetation; $K_{community}$, $Ca_{community}$, $P_{community}$ and $Mn_{community}$: nutrient concentration in uninvaded vegetation.*

From a much larger number of significant multiple regressions (data not shown), the following combinations yielded the five highest r^2 values:

$B_{invader}$=0.589-1.21×10^{-3}SLA+0.0410$K_{community}$ (r^2=0.778, p<0.001)

$B_{invader}$=0.983+0.426R_{Ca}-2.10$Mn_{community}$ (r^2=0.770, p<0.001)

$B_{invader}$=1.02-1.19×10^{-3}SLA+0.823$B_{community}$ (r^2=0.705, p<0.001)

$B_{invader}$=0.709-1.10×10^{-3}SLA+0.0423$Ca_{community}$ (r^2=0.702, p<0.001)

$B_{invader}$=0.639-1.20×10^{-3}SLA+0.276$P_{community}$ (r^2=0.683, p<0.001).

The multiple regressions significantly improved the simple regressions on the composing variables (F-test, p<0.05). The significant models were plant as well as ecosystem driven: all combinations of SLA or Mn_{YFEL} with any ecosystem trait were significant, and so were all combinations of $B_{community}$, $Mn_{community}$ or $Ca_{community}$ with any plant trait. The best regressions of $B_{invader}$ in spring and summer were both dominated by SLA, but they differed in ecosystem traits, possibly because a larger set of variables was used. However, trait combinations that were tested both in spring and in summer, yielded similar r^2. When comparing $H_{invader}$ and $B_{invader}$ in summer, the best five regressions had few variables in common: regressions of $B_{invader}$ included SLA or the resorption index of Ca, whereas the regressions of $H_{invader}$ included five other resorption efficiencies; $B_{community}$ was common to all five models of $H_{invader}$ while it was part of only one $B_{invader}$ model.

2.2 Seed production

Ten simple regressions were significant (Figure 6 and 7), two on ecosystem traits (RFR ratio in spring and $P_{community}$), eight on plant traits (summer: LMR, α and both in spring and summer: C_{YFEL}, height, aboveground biomass). The plant traits explained seed production to a greater extent, up to a maximum of 46%. All traits had a positive effect on seed production except for LMR and RFR ratio. The results suggest that plants with high sexual reproductive capacity, are tall and invest in high stem but not high leaf mass, have high carbon concentration in young leaves and high α, and occur preferentially in P-rich vegetation that greatly reduces light. Nutrient concentrations, whether in young or senescent leaves, in vegetation or soil of uninvaded sites, never explained seed production except for $P_{community}$. Nor did seed mass or any of the resorption efficiencies or diversity-related traits. Traits measured both in spring and summer explained seed production to a similar extent, except for LMR and α.

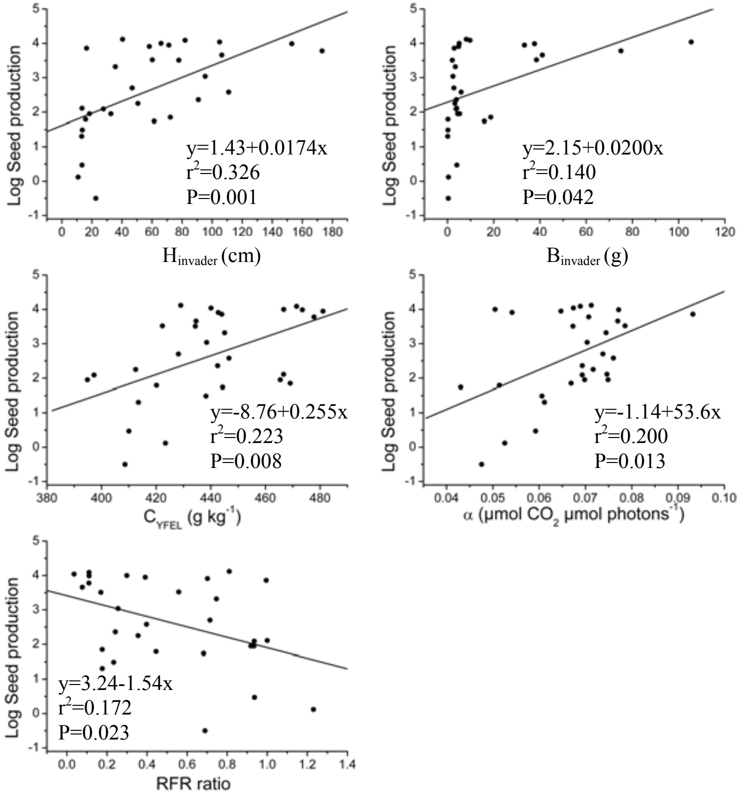


Figure 6 *- Significant simple regressions of invader seed production on spring plant or ecosystem traits. Each symbol represents one species × site combination. $H_{invader}$, $B_{invader}$: height or shoot biomass of the invader; CYFEL: carbon concentration in youngest fully expanded leaves; α: apparent quantum efficiency; RFR ratio: ratio of red:far red ratio at ground level to top of the canopy.*

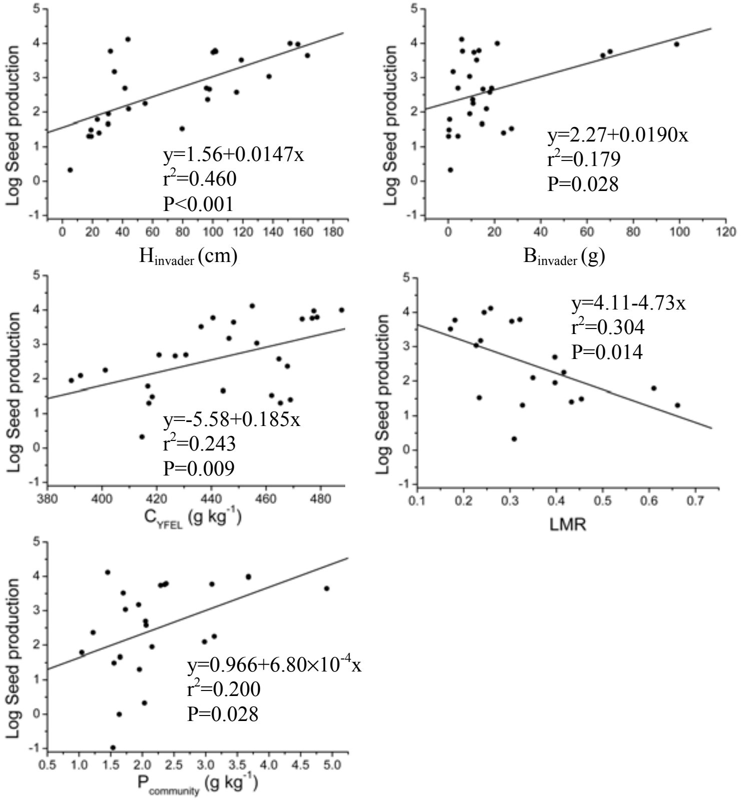


Figure 7 - *Significant simple regressions of invader seed production on summer or annual plant or ecosystem traits. Each symbol represents one species × site combination. $H_{invader}$, $B_{invader}$: height or shoot biomass of the invader; CYFEL: carbon concentration in youngest fully expanded leaves; LMR: leaf mass ratio; Pcommunity: phosphorus content in uninvaded vegetation.*

Sixteen percent of all multiple regressions were significant (data not shown), of which about half had a significantly higher r^2 than the corresponding best simple regression model. Most significant multiple regressions included a trait already significant in simple regressions, however, this does not guarantee high r^2, as the two best models had corresponding nonsignificant simple regressions. The predictive capacity of element concentrations in senescent leaves exceeded that of young leaves. Summer traits usually surpassed spring traits in r^2. The predictive value of SLA and the photosynthetic variables (except for α), was negligible in spring. Surprisingly, so was seed mass, as many scientists did find a significant relationship with seed production. The following combinations yielded the ten highest r2 values ($p<0.001$):
Seed production=5.32-2.83×10-4Mgsenescent-5.96×10-2C:Nsoil (r^2=0.848)
Seed production=4.87-2.92×10-4Mgsenescent-7.83×10-2Corg, soil (r^2=0.775)
Seed production=1.43+1.84×10-2Height-3.57×10-2Corg, soil (r^2=0.754)
Seed production=1.53+1.75×10-2Height-1.46×10-2C:Nsoil (r^2=0.729)
Seed production=1.23+1.80×10-2Height-9.02×10-3Ccarbo, soil (r^2=0.721)
Seed production=4.27-1.21×10-3Fesenescent-7.46×10-2Corg, soil (r^2=0.716)
Seed production=4.33-2.73×10-4Mgsenescent-2.11×10-3Mncommunity (r^2=0.671)
Seed production=2.80-3.26×10-4Mgsenescent+6.19×10-4Pcommunity (r^2=0.664).
Seed production=4.35-1.01×10-3Fesenescent-4.28×10-2C:Nsoil (r^2=0.644)
Seed production=4.56-4.69×10-3Mnsenescent-1.32×10-2Zncommunity (r^2=0.633)
These models significantly improved the simple regressions on the composing variables (F-test, $p<0.05$). Apparently, height and element concentrations in senescent leaves, in uninvaded vegetation, or in the soil underneath are essential in explaining seed production. Only height and Pcommunity were also significant in simple regression and influenced seed production positively.

Impact

All correlations between, on the one hand one of the 80 impact measures, and on the other hand one of the plant or ecosystem traits, were tested (Tables 1 and 2).

***Table 1 -** Correlation coefficients of soil impact differences (invaded – uninvaded, upper row) on plant or ecosystem traits (second column). Significance levels: p<0.01 (bold), p<0.05 (not bold), otherwise not significant. Number of sites between brackets.*

		pH_{H2}	pH_{KCl}	Cu_{soil}	K_{soil}	Mg_{soil}	Mn_{soil}	P_{soil}	Zn_{soil}	N_{soil}	$C:N_{soil}$
Spring	α										-0.501(21)
	R_d	0.508(22)		**0.703**(22)			0.528(22)				
	I_c	-0.475(22)		**-0.640**(22)			-0.440(22)				
	P_{max}										**-0.577**(21)
	N_{YFEL}								0.432(22)		
	$C:N_{YFEL}$		-0.445(22)						-0.440(22)		
	$N_{YFEL,\ area}$										**-0.601**(21)
	$H_{invader}$			-0.462(22)							
	ΔT										**-0.570**(21)
	ΔVPD										-0.465(21)
	PAR ratio										**-0.599**(21)
	RFR ratio										-0.482(21)
Summer	α										-0.504(20)
	P_{max}										**-0.631**(20)
	C_{YFEL}		-0.455(21)								
	$B_{invader}$			**-0.685**(21)			-0.438(21)				
	ΔT										-0.478(20)
	Δe		**-0.584**(21)							-0.513(20)	
	Par ratio										**-0.615**(20)
Annual	$C_{tot,\ soil}$					-0.529(22)					0.442(21)
	$N_{tot,\ soil}$										0.488(21)
	Mn_{soil}						**-0.559**(21)				
	P_{soil}			**-0.653**(21)	-0.526(21)		**-0.561**(21)	**-0.604**(21)			
	pH_{H2O}										-0.532(21)
	pH_{KCl}										-0.532(21)

CYFEL, NYFEL and NYFEL, area: carbon, mass-based nitrogen and area-based nitrogen concentration in youngest fully expanded leaves; C:NYFEL: carbon:nitrogen ratio in youngest fully expanded leaves; Pmax, Rd, Ic and α: light-saturated photosynthetic rate, dark respiration rate, light compensation point and apparent quantum efficiency; $B_{invader}$ and $H_{invader}$: invader aboveground biomass and height; PAR ratio or RFR ratio: ratio of photosynthetically active radiation or red:far red ratio at ground level to top of the canopy; ΔT, ΔVPD and Δe: difference in temperature, vapor pressure deficit and vapor pressure between ground level and top of the canopy; Ctot, soil, Ntot, soil, Psoil and Mnsoil: total carbon, total nitrogen and phosphorus and manganese concentration in soil of uninvaded plots. pH_{H2O} and

pH_{KCl}: pH in soil of uninvaded plots.

***Table 2 -** Correlation coefficients of soil impact ratios (invaded/uninvaded, upper row) on plant or ecosystem traits (second column). Significance levels: p<0.01 (bold), p<0.05 (not bold), ns (not significant). Number of sites between brackets.*

		pH_{H2O}	pH_{KCl}	K_{soil}	Mg_{soil}	Mn_{soil}	P_{soil}	Zn_{soil}	$C_{org, soil}$
Spring	α								0.455(21)
	R_d	0.533(21)	0.461(21)						
	I_c	-0.493(22)	-0.531(21)						
	P_{max}								0.439(21)
	N_{YFEL}							0.487(21)	
	$C:N_{YFEL}$							-0.446(21)	
	$H_{invader}$							0.489(21)	
Summer	α	-0.469(21)							
	R_d								-0.463(20)
	P_{max}								**0.646(20)**
	Δe		-0.524(20)	0.450(21)	0.466(21)				
Annual	CU_{YFEL}								0.465(21)
	P_{soil}					-0.434(21)	-0.436(21)		

CuYFEL and NYFEL: copper and nitrogen (mass-based) concentration in youngest fully expanded leaves; C:NYFEL: carbon:nitrogen ratio in youngest fully expanded leaves; Pmax, Rd, Ic and α: light-saturated photosynthetic rate, dark respiration rate, light compensation point and apparent quantum efficiency; $H_{invader}$: invader height; Δe: difference in vapor pressure between ground level and top of the canopy; Psoil: phosphorus concentration in soil of uninvaded plots.

For statistical reasons, only correlations based on 20 or more sites were considered. As a consequence, all biomass-based impacts were left out. The correlations for impact differences were more numerous and significant than those for impact ratios. Plant as well as ecosystem traits contributed to both groups of correlations, implying that invader traits, as well as traits of the ecosystem prior to invasion, predetermine to what extent the invader changes the soil characteristics.

Concerning impact ratios, the highest r was found between the ratio of Corg, soil and Pmax (summer). For impact differences, the best model contained the difference in Cusoil and Rd (spring).

3. Discussion

$H_{invader}$ and $B_{invader}$

Summarizing the results of the simple regressions on plant traits in order to answer question 1, we conclude that large or productive invaders were characterized by a high CYFEL and NYFEL, area, a low MnYFEL, low SLA, and values of the photosynthetic variables typical of unshaded plants (α excepted). Question 2 can be answered as follows: ecosystems invaded by large or productive invaders were characterized by a nutrient-rich (K, Ca, P, not Mn) and productive vegetation, with humid, cool and shaded conditions at ground level relative to top of the canopy. The combinations of traits that maximized the explained variance (question 3) included the plant traits NYFEL, area, MnYFEL, SLA, Rd and the element resorption indices (Mn, P, Mg, K, Zn), and the ecosystem traits RFR ratio, ΔT, $B_{community}$ and the element concentrations (K, Ca, P, Mn) in the uninvaded vegetation. With up to 80% of the variance in invader growth explained, the approach of combining plant and ecosystem traits, seems promising. In most cases, trait influences were additive and conservative in the sense that (i) two traits that were significant in simple regressions, generally resulted in significant multiple regressions and vice versa, and (ii) the nature of the contributions of the traits (positive or negative) remained the same between the simple and multiple regressions. A specific case were the resorption indices, which were significant in none of the simple regressions, but frequently took part in the best multiple regression models (positive effect except for Zn). This can be understood from the fact that three-dimensional scores that make up a plane (significant multiple regression), need not yield a straight line when projected on a two-dimensional surface (nonsignificant simple regression). The case of the resorption indices suggests that "matches" exist between plant and ecosystem traits, and demonstrates again the surplus value of multiple - as opposed to simple - regressions.

Table 3 *- Significant simple regressions of invader height ($H_{invader}$) or invader aboveground biomass ($B_{invader}$) on a plant or ecosystem trait*

Success measure	Spring data set		Summer data set	
	Plant trait	Ecosystem trait	Plant trait	Ecosystem trait
$H_{invader}$	C_{YFEL} (+) Mn_{YFEL} (-)	PAR ratio (-) RFR ratio (-) ΔT (-) ΔVPD (-)	C_{YFEL} (+) Mn_{YFEL} (-)	PAR ratio (-) ΔT (-) $B_{community}$ (+) $K_{community}$ (+)
$B_{invader}$	C_{YFEL} (+) Mn_{YFEL} (-) SLA (-) α (+)		C_{YFEL} (+) Mn_{YFEL} (-) SLA (-) α (+) R_d (-) I_c (+) $N_{YFEL, area}$ (+)	$B_{community}$ (+) $K_{community}$ (+) $Ca_{community}$ (+) $P_{community}$ (+) $Mn_{community}$ (-)
Seed production	C_{YFEL} (+) $H_{invader}$ (+) $B_{invader}$ (+) α (+)	RFR ratio (-)	C_{YFEL} (+) $H_{invader}$ (+) $B_{invader}$ (+) LMR (-)	$P_{community}$ (+)

Nature of the relationship between brackets. CYFEL, MnYFEL and NYFEL, area: carbon and manganese (mass-based) and nitrogen (area-based) concentration in youngest fully expanded leaves; SLA: specific leaf area; Rd, Ic and α: dark respiration rate, light compensation point and apparent quantum efficiency; PAR ratio or RFR ratio: ratio of photosynthetically active radiation or red:far red ratio at ground level to top of the canopy; ΔT and ΔVPD: difference in temperature and vapor pressure deficit between ground level and top of the canopy; $B_{community}$: aboveground biomass of uninvaded vegetation; Kcommunity, Cacommunity, Pcommunity, Mncommunity: nutrient concentration in aboveground uninvaded vegetation.

Photosynthetic characteristics, especially Pmax, are often included in studies of invader biology. A high Pmax implies either a high efficiency at utilizing light energy, or abundant carboxylating enzymes (Field & Mooney, 1986; Larcher, 1995). Although we observed a large variation in Pmax, we could not relate it to invader growth, similar to Smith & Knapp (2001) who did not observe significant differences in Pmax in one of the few studies comparing successful and unsuccessful invaders. However, our productive invaders did display a significant pattern in other gas exchange parameters: high Rd and Ic unexpectedly coincided with high α (Figure 4 and 5), a hybrid pattern between sun and shade leaves. During the seedling stage, productive invaders may have had to cope with the surrounding vegetation casting shade (cf. high $B_{community}$), which they had outgrown by the time we measured photosynthesis. Possibly the combination of high Rd and Ic, but high α, is the best evolutionary compromise for an invader to be productive both in the low light environment of the early growth stages and the sunny conditions (not shown) experienced by the YFEL of mature plants. For predictive purposes, however, the practicability of the photosynthetic variables is limited, because of the small r^2's and their specialized measurement.

Across our selection of species and sites, productive invaders were characterized by low SLA. This agrees with the general finding that species with a low SLA occur in high light (Poorter & Van Der Werf, 1998; Shipley, 2000), since the YFEL of our productive invaders were typically above the canopy (cf. above). In contrast, the observed low SLA values in productive invaders do not seem to agree with the positive relationship that is found between SLA and relative growth rate in most experimental studies (Poorter & Van Der Werf, 1998). Shipley (2002) attributed this positive relationship to the low light intensities in controlled experiments and found a negative relationship under more realistic intensities, as observed in our study. However, comparing specifically invasive exotic and non-invasive exotic species, Lake & Leishman (2004) observed higher SLA in the former, whereas Smith & Knapp (2001) found no difference. In these studies, range expansion was used as success measure, which suggests that SLA might be positively coupled to success at regional scale, but negatively to local success as governed by productivity (Nijs *et al.*, 2004). Given the ease of determining SLA, and its high explanatory power - particularly in our multiple regressions - SLA could be a suitable predictor candidate of height and aboveground biomass.

Several aspects of the carbon and mineral nutrient relations of invaders and invasible ecosystems also contributed to explaining invader performance. For example, the higher carbon concentrations in leaves of tall or productive invaders may reflect the greater structural needs of older (longer life span) or more rigid leaves/stems (e.g. of *F. japonica*, *P. serotina* and *R. rugosa*), and may arise from higher concentrations of carbon-rich cell wand components such as lignin and cellulose (Poorter & Villar, 1997). A striking aspect of the nutrient characteristics was the fact that tall or productive invaders had low MnYFEL (Figure 2 to 5), and occurred themselves in ecosystems with low Mncommunity (Figure 5). Considering that organic matter complexes with Mn, a high amount of organic matter owing to large $B_{invader}$ and $B_{community}$ may have decreased the availability of Mn to the vegetation. Additionally, low soil pH is known to limit (invader) cover and biomass (Owen & Marrs, 2000) and to alien invasive species Mn availability (Page, 1961; Andrade *et al.*, 2002). The combination of both pH-induced effects may add to the negative relationship between growth and Mn. Low Mn might therefore serve as a cautionary notice in screening out successful - in terms of rapid invader growth - invasions. Besides CYFEL, NYFEL, area and MnYFEL, no other element concentrations in

YFEL predicted invader growth, except when combined with ecosystem traits that were already significant in simple regressions. The nutrient resorption indices, on the other hand, were included in some of the best multiple regression models. In infertile environments, nutrients can be conserved (higher residence time in the plant) by extending leaf life span and/or by minimizing the nutrient concentration of abscised leaves (Eckstein *et al*., 1999). Surprisingly, high resorption of nutrients (Zn excepted) related to slow invader growth in the current study. Apparently, small-stature or unproductive invaders occurred in infertile environments, where resorption is critical. Though these resorption indices require leaf sampling and specialized analyses twice a year, they have high explanatory power and therefore are potential predictors.

Tall and productive invaders occurred themselves in productive communities characterized by high concentrations of K, Ca and P (Figure 4 and 5). Combined with a low resorption (cf. above), these factors would give rise to the release of large amounts of nutrients in the ecosystem at the end of the season, which may have promoted invader growth at our productive sites. For the positive relationship between $B_{invader}$ and $Ca_{community}$, an additional explanation could be the species composition of the uninvaded ecosystem. Dicots generally have higher shoot Ca concentrations than monocots (Broadley *et al*., 2003), so ecosystems invaded by productive invaders may be dicot-rich. The presence of tall or productive invaders in productive ecosystems might also arise from mechanisms not related to nutrients. For example, dense vegetation (high $B_{community}$) may select for species capable of growing tall in order to capture enough light, or invader species may maximize their height at sites where light transmission is low. The latter effect would be mediated by phytochrome and activated by low red:far red ratios in the shade. Contrary to our findings, Foster *et al*. (2002) linked high invasibility to high light transmission and low community biomass, while De Gruchy *et al.* (2005) found that communities with low total biomass contained highest alien biomass. However, the first authors expressed invasibility as the colonisation success of sown species, which includes germination and species survival, and these processes may have other light optima than invader growth, and the second group of authors did not use individual, but total alien biomass, which incorporates invader abundance. Therefore, whether nutrients or light availability drive invader growth, the high explanatory power and the easy quantification of $B_{community}$, indicate potential for prediction purposes.

Finally, past studies have yielded contrasting relationships between species richness and invasion success. In small-scaled, controlled experiments, this relationship was often negative, whereas large-scaled, natural invasibility studies along diversity gradients usually concluded the opposite (Li *et al*., 2005). At small scales, high richness in plant communities leads to strong complementarity in resource use, and consequently to low resource availability for invaders. In spite of the small scale at which we determined both richness and success, our results did not endorse a negative relationship: richness, evenness, nor diversity influenced individual invader growth significantly. Possibly, the aforementioned mechanism is too weak relative to the influence of extrinsic factors in the field. This would be consistent with the low variance explained by richness even in synthesized communities (Levine, 2000).

Seed production

Plant fitness is obviously bound down by intrinsic limitations. However: our data show that seed production varies between sites, because an invasible ecosystem may be more favourable for the invader than a resistant ecosystem, i.e. may induce greater seed production. Trait influences were usually additive and conservative in the sense that: (i) the nature of the contribution of the traits (positive or negative) remained the same between simple and multiple regressions, and (ii) two traits that were significant in simple regressions, generally resulted in significant multiple regressions. However, all ten best multiple regressions comprised at least one trait not significant in simple regressions, which demonstrates the surplus value of matching plant and ecosystem traits. Whereas plant and ecosystem traits explained invader height and aboveground biomass to a similar extent (see above), seed production was predicted optimally by plant traits. Different traits were of similar use for prediction.

Life history theory prophesies environmental-dependent compromises between the different factors contributing to plant success: some vegetative growth may be sacrificed for reproductive growth, seed number may be reduced to increase seed size (Aarssen & Jordan 2001). In view of the widely valid negative relationship between seed production and seed mass (Shipley & Dion, 1992; Greene & Johnson, 1994; Jakobsson & Eriksson, 2000; Henery & Westoby, 2001; Leishman, 2001), the absence of such a trade-off in our data came as a surprise. However, this relationship has been shown to be allometric: a larger species with more resources to allocate may produce more or larger seeds, or both, thus possibly obscuring any existing trade-off (Aarssen & Jordan, 2001). On the other hand, precisely the ability to combine high seed production with high seed mass, may be an invader trait.

Not surprisingly, plant size - particularly height - influenced seed production positively. Size-dependent variation in (absolute) reproductive effort is indeed theoretically and empirically amply demonstrated (Samson & Werk, 1986; Shipley & Dion, 1992; Susko & Lovett-Doust, 2000; Aarssen & Jordan, 2001; Willis & Hulme, 2004), both at the between-species and within-species level. Larger plants may flower earlier or longer (Ollerton & Lack, 1998), or produce more female flowers (in diphasic species, Susko & Lovett-Doust, 2000), or have lower seed abortion (more mature fruits). In addition, many species show a critical threshold size for flowering (Samson and Werk, 1986). High resource availability - supposed to enhance invasion

(Alpert *et al.*, 2000) - might influence both plant size and seed production positively, possibly via the concurrence of large plant size and increased branchiness or stem elongation, which may improve the chance of lateral inflorescences (Willis & Hulme, 2004). On the other hand, life-form or intrinsic structural layout may affect seed production more than plant size (Aarssen & Jordan, 2001). E.g. reproductive output was highest in perennials (*F. japonica*, *S. inaequidens*, *S. gigantea*).

Seed production was negatively related to RFR ratio and LMR. We believe shade-avoidance caused these relationship: to increase light interception (see above) stems elongated at the expense of lateral growth. This resulted in great height and aboveground biomass (related to great seed production), and reduction of the fraction leaf mass (LMR, Givnish, 1988). We hypothesized that the mechanistic support required to keep a tall plant erect, is reflected in high CYFEL (see above). This may have caused the positive relationship between seed production and CYFEL, as high reproductive and vegetative output concurred.

Traits related to mineral nutrients had high explanatory power as regards plant size (see above). This was notably different in seed production, to which only Pcommunity could be related. Apparently, seed production is high in P-rich ecosystems. In the best multiple regressions, low mineral nutrient concentrations (Fe, Mg and Mn) in senescent leaves, contributed to high seed production. It appears that a high reproductive yield is associated with low nutrient concentrations in abscising leaves, which could be a nutrient conservation strategy (Eckstein *et al.*, 1999). This contradicts at first sight with the positive relationship found between growth and nutrient resorption. Here however, absolute concentrations play, instead of ratios.

In multiple regressions, several aspects of the soil carbon household influenced seed production substantially: low organic C - whether or not per unit Nsoil - and carbonate C concurred with high seed production. Annapurna & Singh (2003) too found high seed production for sandy, organic carbon-poor soils.

Impact

Several impact measures correlated with traits (table 1 and 2). Our set of species frequently had impact on soil pH (see section 2): *I. parviflora* and *P. serotina* typically increased pH, whereas *F. japonica*, *I. glandulifera*, *S. inaequidens* and *R. rugosa* lowered pH. Invaders that increased soil pH (H20 or KCl) displayed a hybrid pattern between sun and shade leaves typical of small unproductive invaders (low Rd, Ic and α, see above). Ascribing the pH effect to light or biomass is however premature since impact on pH was not directly related to $H_{invader}$, $B_{invader}$, PAR ratio or RFR ratio.

Plant invasions usually increased soil K, Mg and Mn (see section 2). Few predictores were found for impact on soil K and Mg. However, differences in Cusoil and Mnsoil, correlated with several plant and ecosystem traits. Similar to the effects on pH-impact, increases in Cusoil and Mnsoil correlated with low Rd, Ic and α. We ascribed this photosynthetic behaviour to small invaders (see above). The negative effect of invader growth ($H_{invader}$ and $B_{invader}$) on Cusoil and Mnsoil agrees with this hypothesis and indicates that small invaders changed the concentrations of these nutrients most strongly. Possibly, ecosystems invaded by tall invaders were already productive (see results for $H_{invader}$ and $B_{invader}$), whereas small invaders may have invaded bare ground.

Soil organic carbon showed no clear pattern, and soil C:N usually increased due to the invasion (see section 2). Photosynthesis and light related traits indicate that ecosystems with low light transmission, where invaders with low Pmax and Ic settled, lowered Corg, soil, but alien invasive species C:Nsoil. This alien invasive species surprise, as the two indicators of soil decomposition rate (Corg, soil, C:Nsoil) point at contradictory conclusions. When light transmission was high, the opposite occured. Furthermore, differences in C:Nsoil were highest when low pH-soils were invaded.

SECTION 2: IMPACT OF PLANT INVASIONS ON ECOSYSTEM PROPERTIES

1. Materials and methods

1.1 Site selection

Two to six sites were selected for each species in ecosystems with contrasting resident vegetation structure and composition, representing the range of habitats colonised by the study species in Belgium. The sites fulfilled the following conditions: 1) having well-established, and still expanding populations of the target species surrounded by native uninvaded vegetation, 2) having sufficiently homogeneous soil. Site selection tried to minimise the probability of differences existing before the invasion event. To that end, invaded and control uninvaded plots selected in each site were in the same topographic situation and had the same soil texture (See Vanderhoeven *et al.*, 2005 for methods). Moreover, the uninvaded control plots were located as close as possible to the front of expansion of the invader. We can therefore assume any systematic differences observed between invaded and uninvaded soils are most likely due to difference of vegetation. Due attention will be paid in the discussion to the possibility of pre-existing differences.

1.2 Soil sampling

At each site, six 1-m² plots were located in invaded patches and six 1-m² plots were located in adjacent, uninvaded vegetation.

Soil was sampled from February to April 2004. In each plot, five soil cores (0-10 cm depth, litter discarded) were collected with a soil borer (4 cm in diameter, one core at each corner of the square and one core at the centre of the square). These five cores were mixed up into a single bulk sample for each plot. Soil samples were air-dried until constant weight and sieved (< 2 mm).

1.3 Soil analysis

The following parameters were assessed on each sample: Soil pH, exchangeable protons and aluminium (1M KCl extraction and titration, for acidic soils only), exchangeable Ca, Mg, K, Cu, Zn, Mn and P (1M CH_3COONH_4 pH 4.65 extraction and ICP-AES determination). Ca was not determined for samples containing free $CaCO_3$. Cation exchange capacity (CEC = $[Ca^{2+}] + [K^+] + [Mg^{2+}] + [H^+] + [Al^{3+}]$) and base saturation rate (Bs) were thereafter computed (Bs = $([Ca^{2+}] + [K^+] + [Mg^{2+}])/CEC$) except for carbonated soils. Organic C, N content and C/N were also assessed. For technical details, see Vanderhoeven *et al.* (2005).

1.4 Biomass sampling and analysis

Aboveground biomass was harvested in invaded and control plots at the peak of biomass (between June and August) for 6 of the 9 species (not *H. mantegazzianum, Prunus serotina and Rosa rugosa*) on the same plots as for soil sampling. The plant samples were dried at 70° C to constant weight. A representative subsample was finely ground (0.12 mm) and analysed for Ca, Mg, K, P, Mn, Pb, Zn and Cu concentration (550° C calcination, HCl dissolution of the ashes and ICP-AES determination). C and N content were assessed using a dry combustion C/N analyser (NC-2100, Carlo Erba Instruments). The aboveground nutrient stock (mg m^{-2}) was then calculated as the product of mineral nutrient concentration and biomass. For technical details, see Vanderhoeven *et al.* (2005).

1.5 Statistical analyses

For soil parameters, a two-way ANOVA was performed for each species on all sites pooled (species per species), with ‘site’ (fixed) and ‘invasion’ (fixed) as main effects and 'site x invasion' as interaction effect. In this analysis, a significant site x invasion interaction indicates that impacts vary depending on site. Secondly, for soil and plant parameters, a global three-way nested ANOVA was applied to all sites and all species pooled with species (fixed), site (random, nested in species) and invasion (fixed) as main effects and species X Invasion and site (species) X invasion as interaction effects. Log transformation was applied before ANOVA when necessary. Then for soil parameters, for each species in each site, mean values of all parameters were compared between invaded and uninvaded plots by means of t-tests. In this report, we only show the results of the t-tests for K, Mg, P and Corg in sites invaded by *F. japonica*. Statistical analyses were performed with Statistica 7.1 software (StatSoft Inc. 2005).

2. Results

Soil

able 4- *Summary of alien invasive species impact on soil parameters: an arrow indicates a significant (p<0.05) invasion effect in the two-way ANOVA (Site, Invasion) and its direction: ↑= invaded > uninvaded, ↓ = invaded < value, - = no significant impact*

	Fallopia japonica	*Solidago gigantea*	*Impatiens glandulifera*	*Impatiens parviflora*	*Senecio inaequidens*	*Rosa rugosa*	*Prunus serotina*	*Heracleum mantegazzianum*	*Polemonium caeruleum*
pH	↓	-	↓	↑	↓	↓	↑	-	-
Ca	n.d.	n.d.	n.d.	↑	n.d.	n.d.	↑	n.d.	-
Cu	↑	-	-	-	-	-	↓	-	-
K	-	-	-	-	↑	↑	-	-	-
Mg	↑	-	↑	↑	↑	↑	-	↓	-
Mn	↑	-	↑	-	-	-	-	-	-
P	-	↑	-	↑	-	-	-	-	-
Zn	↑	-	-	-	-	-	-	-	-
H	n.d.	n.d.	n.d.	↓	n.d.	n.d.	-	n.d.	-
Al	n.d.	n.d.	n.d.	↓	n.d.	n.d.	-	n.d.	-
CEC	n.d.	n.d.	n.d.	↑	n.d.	n.d.	-	n.d.	-
Sat	n.d.	n.d.	n.d.	↑	n.d.	n.d.	↑	n.d.	-
Corg	-	-	↑	-	-	-	-	↓	↓
N	-	-	↓	-	↓	↑	-	↓	↓
C/N	-	-	↑	↓	↑	-	↑	-	↑

n.d. = not determined.

Alien invasive species often had an impact on soil pH (Table 4). The two-way ANOVA showed a significant invasion effect for 6 of the 9 species but not always in the same direction (Figure 8).

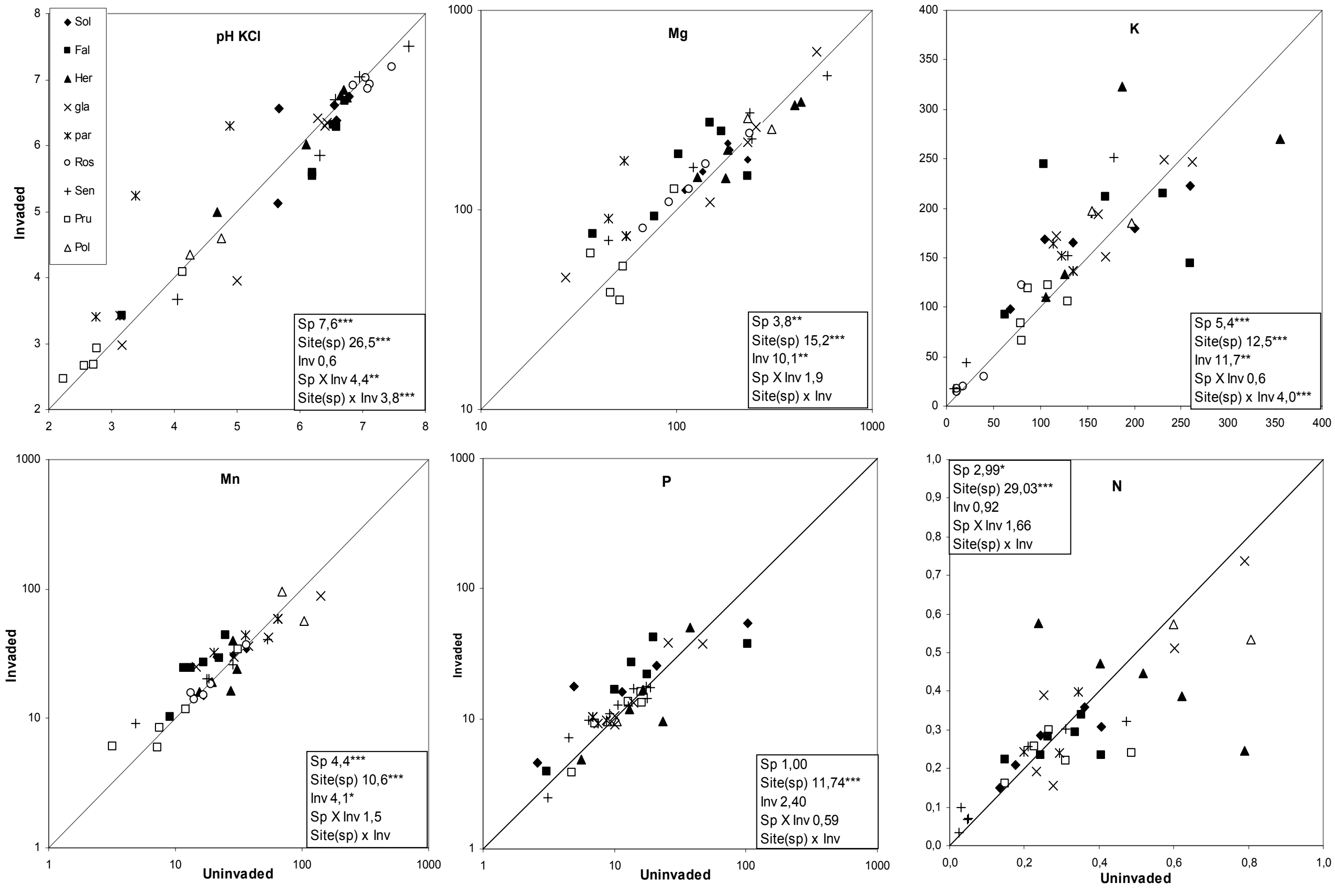


***Figure 8**: Soil chemical parameters in invaded and uninvaded plots. Values are in mg kg^{-1} except for pH (no unit) and N (in %). The line denotes equal value for invaded and control plots. Value above the line indicates increased value in invaded plot. The results of the three-way ANOVA are indicated: F values and significance level : * P < 0.05; ** P < 0.01; *** P < 0.001. ♦ S.gigantea, ■ F. japonica, ▲ H. mantegazzianum, ∗ I. parviflora, X I. glandulifera, ∆ P.caeruleum, ○ R. rugosa, + S. inaequidens, □ P. serotina.*

***Table 5** - Three-way ANOVA of soil parameters: 9 species sampled in 2-6 sites/species, comparison of adjacent invaded/uninvaded plots. Log transformed data except pH and Corg.*

	df[1]	pH	Ca	Cu	K	Mg	Mn	P	Zn	N	Corg	C/N
Species	8	7,56 ***	3,23 *	1,53	5,43 ***	3,79 **	4,44 ***	1,00	2,18	2,99 *	2,78*	2,96 *
Site(species)	33	26,48 ***	10,82 ***	23,16 ***	12,54 ***	15,15 ***	10,62 ***	11,74 ***	45,36 ***	29,03 ***	22,84 ***	23,70 ***
Invasion	1	0,64	3,16	0,00	11,68 **	10,06 **	4,14 *	2,40	2,33	0,92	0,22	0,94
Sp X Inv	8	4,35 **	1,97	1,42	0,57	1,91	1,45	0,59	0,78	1,66	0,92	1,35
Site(Sp) X Inv	33	3,81 ***	4,61 ***	3,45 ***	4,03 ***	2,91 ***	2,51 ***	5,05 ***	2,31 ***	3,42 ***	3,18 ***	4,23 ***

df = degree of freedom, [1]: df for site (species) and site (species) X Invasion for Ca = 13 and for N, Corg and C/N = 29

F values and. significance level : * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Soil pH generally increased in sites invaded by *I. parviflora* and *P. serotina* while it generally decreased in sites invaded by *F. japonica*, *I. glandulifera*, *S. inaequidens* and *R. rugosa*. For this reason the invasion effect was not significant in the three-way ANOVA while the species X invasion was (table 5). Ca concentration was only assessed for 3 species established on non carbonated soils. For 2 of them (P. serotina and I. parviflora), Ca availability significantly increased in invaded sites (table 4). K, Mg and Mn availability generally increased under the canopy of alien invasive species (but see the exception with Mg in *H. mantegazzianum*). Figure 8 shows that increased values are more frequent than decreased values for these three elements (K: 31 increases for 11 decreases, Mg: 29 increases for 13 decreases, Mn: 24 increases for 18 decreases). The increase was significant for K in *S. inaequidens* and *R. rugosa*, for Mg in *F. japonica*, *I. glandulifera*, *I. parviflora*, *S. inaequidens* and *R. rugosa* and for Mn in *F. japonica* and *I. glandulifera*. The invasion effect for these three elements was significant in the three-way ANOVA (table 5). The same trend was observed with exchangeable P (Figure 8) with a significant increase for *S. gigantea* (Figure 10) and for *I. parviflora*. The invasion effect in the three way ANOVA was not significant. Soil organic carbon content showed no clear pattern. It increased significantly under *I. glandulifera* while it decreased under *H. mantegazzianum* and *P. caeruleum*. Organic N content significantly increased only under *R. rugosa* while it significantly decreased under *I. glandulifera, H. mantegazzianum, S. inaequidens* and *P. caeruleum*. Soil C/N significantly increased under *I. glandulifera, S. inaequidens, P serotina and P. caeruleum* and significantly decreased under *I. parviflora*.

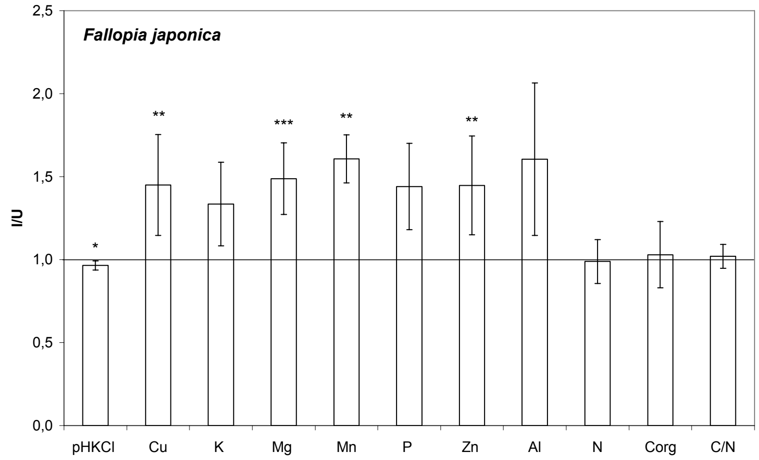


Figure 9*- Comparison of soil properties between invaded and uninvaded plots in sites invaded by F. japonica expressed as the ratio of mean value of invaded plots on mean value of uninvaded plots (I/U). N = 6 sites for all parameters (except Al: 3 sites). Whiskers are standard error. The horizontal line (I/U=1) denotes equal value for invaded and control plots. Value above the line* (I/U>1) indicates increased value in invaded plots. Significance level of Invasion effect in the *two-way ANOVA: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.*

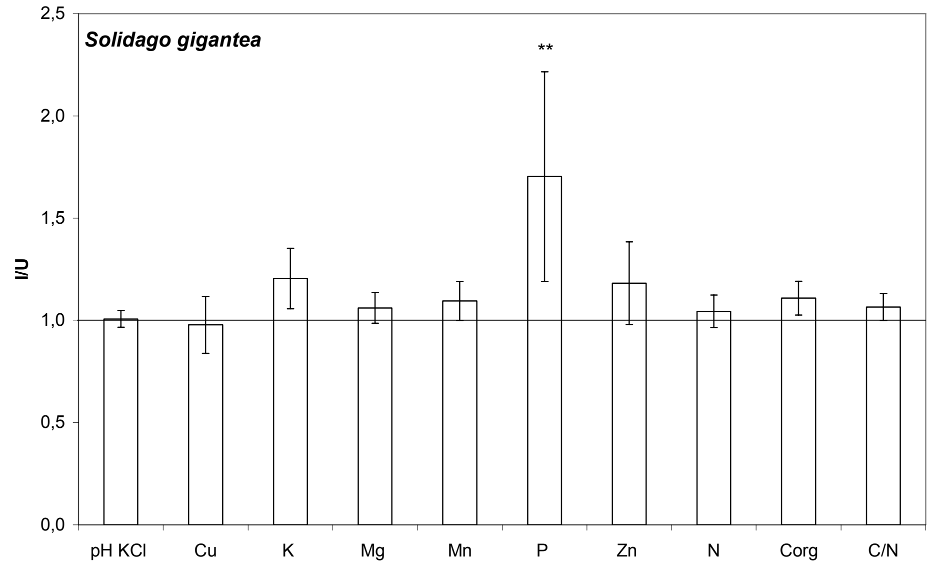


Figure 10*- Comparison of soil properties between invaded and uninvaded plots in sites invaded by S. gigantea expressed as the ratio of mean value of invaded plots on mean value of uninvaded plots (I/U). N = 5 sites for all parameters. Whiskers are standard error. The horizontal line (I/U=1) denotes equal value for invaded and control plots. Value above the line (I/U>1) indicates increased value in invaded plots. Significance level of Invasion effect in the two-way ANOVA: * P < 0.05 ; ** P < 0.01 ; *** P < 0.001.*

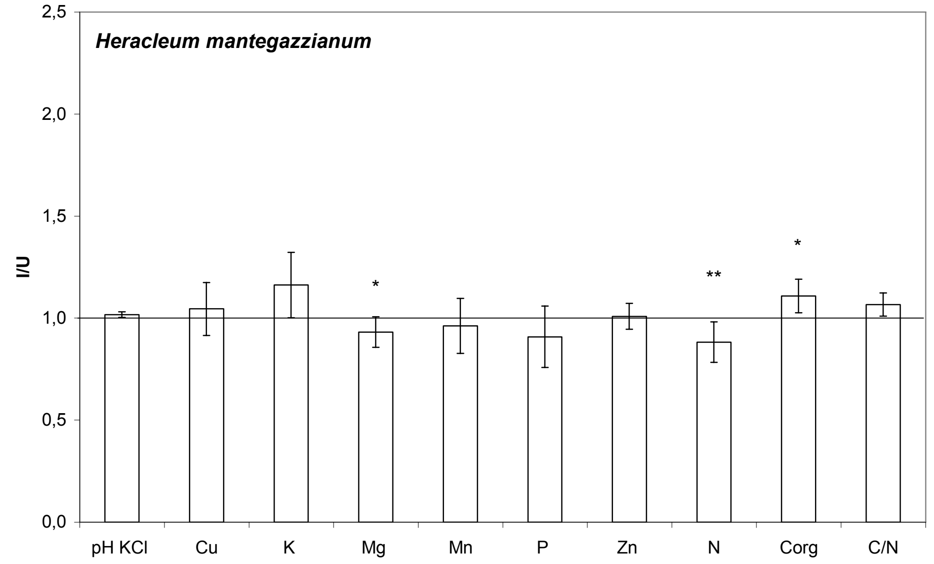


Figure 11*-: Comparison of soil properties between invaded and uninvaded plots in sites invaded by H. mantegazzianum expressed as the ratio of mean value of invaded plots on mean value of uninvaded plots (I/U). N = 5 sites for all parameters. Whiskers are standard error. The horizontal line (I/U=1) denotes equal value for invaded and control plots. Value above the line (I/U>1) indicates increased value in invaded plots. Significance level of Invasion effect in the two-way ANOVA: * P < 0.05 ; ** P < 0.01 ; *** P < 0.001.*

Differences between invaded (I) and uninvaded (U) plots can be expressed as the ratio I/U (1 is the expected value of I/U under the null hypothesis that invasion has no impact). The average value of I/U was calculated for all sites of each species. Only three species with contrasting behaviour (Figure 9, 10 and 11) are shown here.

Figure 9 shows that *F. japonica* had a strong impact on all inorganic parameters of the soil. In particular, there was a slight decrease of pH in invaded plots (I/U ratio < 1) and a general increase in cations and P availability (Cu: +45%, K: +34%, Mg: +49%, Mn: +61%, P: +44%, Zn: +75%). For *S. gigantea* (Figure 10), the only parameter that showed a strong invasion effect was P. For *H. mantegazzianum*, the differences between invaded and uninvaded plots were generally low and rarely significant (only a slight significant decrease for Mg and Mn and a slight increase of Corg).

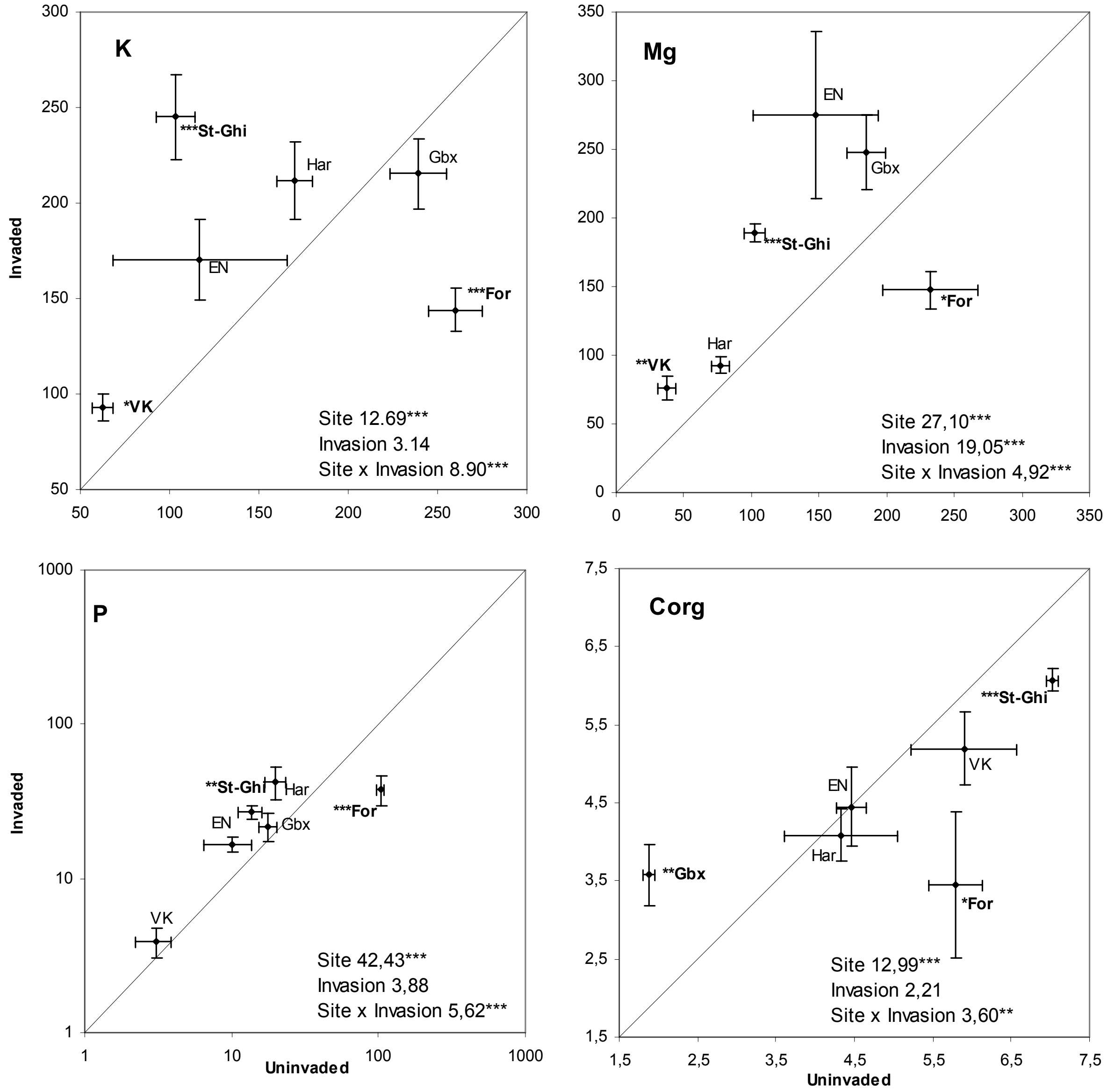


***Figure 12**- Soil chemical parameters (K, Mg, P and Corg) in invaded and uninvaded plots at 6 sites invaded by F. japonica. Values are in mg kg*$^{-1}$ *except for Corg (in %) Whiskers are standard error. The line denotes equal value for invaded and control plots. Value above the line indicates increased value in invaded plot. The results of the two-way ANOVA are indicated: F values and significance level: * P < 0.05 ; ** P < 0.01 ; *** P < 0.001. Sites abbreviations: St-Ghi: Saint-Ghislain, VK: Van Kerm, EN: Enfants noyés, Har: Haren, Gbx: Gembloux, For: Foresterie.*

The results of two-way ANOVAs for K, Mg, P and Corg in sites invaded by *F. japonica* are presented in Figure 12. The site x invasion interaction was significant for these 4 parameters, indicating that impacts of invasion for these parameters varied in direction and/or amplitude depending on local conditions. For instance, K, P and Mg concentrations were significantly higher in invaded plots in site “Ghi” but were lower in site “For”. The site “For” responded very differently to invasion by *F. japonica*, with decreased values of K, Mg and P.

Biomass

Aboveground biomass of the alien invasive species was always higher than the biomass of indigenous uninvaded vegetation. This biomass increase is significant for all species except for *P. caeruleum* (Figure 13). Aboveground biomass in invaded plots of *S. gigantea* was approximately 2 times higher than in uninvaded native vegetation. For *F. japonica*, biomass in invaded plots is on average 6 times higher than in uninvaded plots.

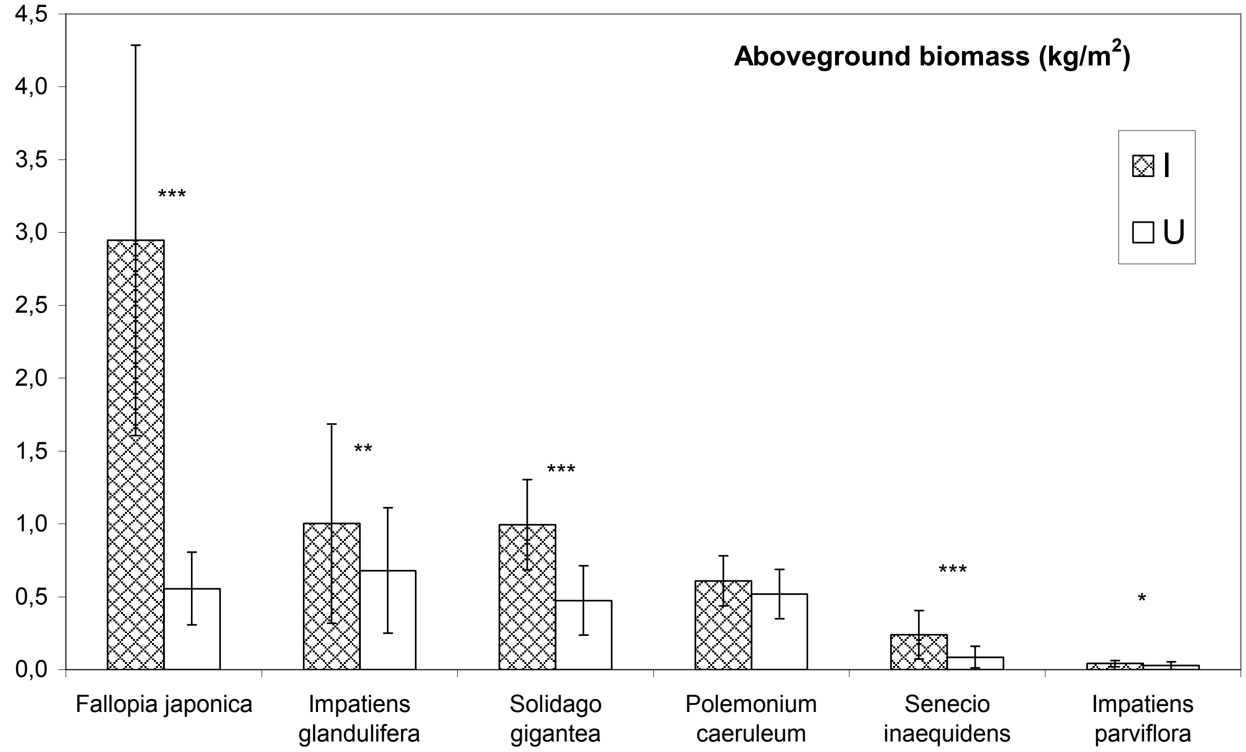


Figure 13 *- Aboveground biomass (kg m^{-2}) in invaded (I) and uninvaded (U) plots. Whiskers are standard error. Significance level of Invasion effect in the two-way ANOVA: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.*

Nutrient concentrations and stocks in plants

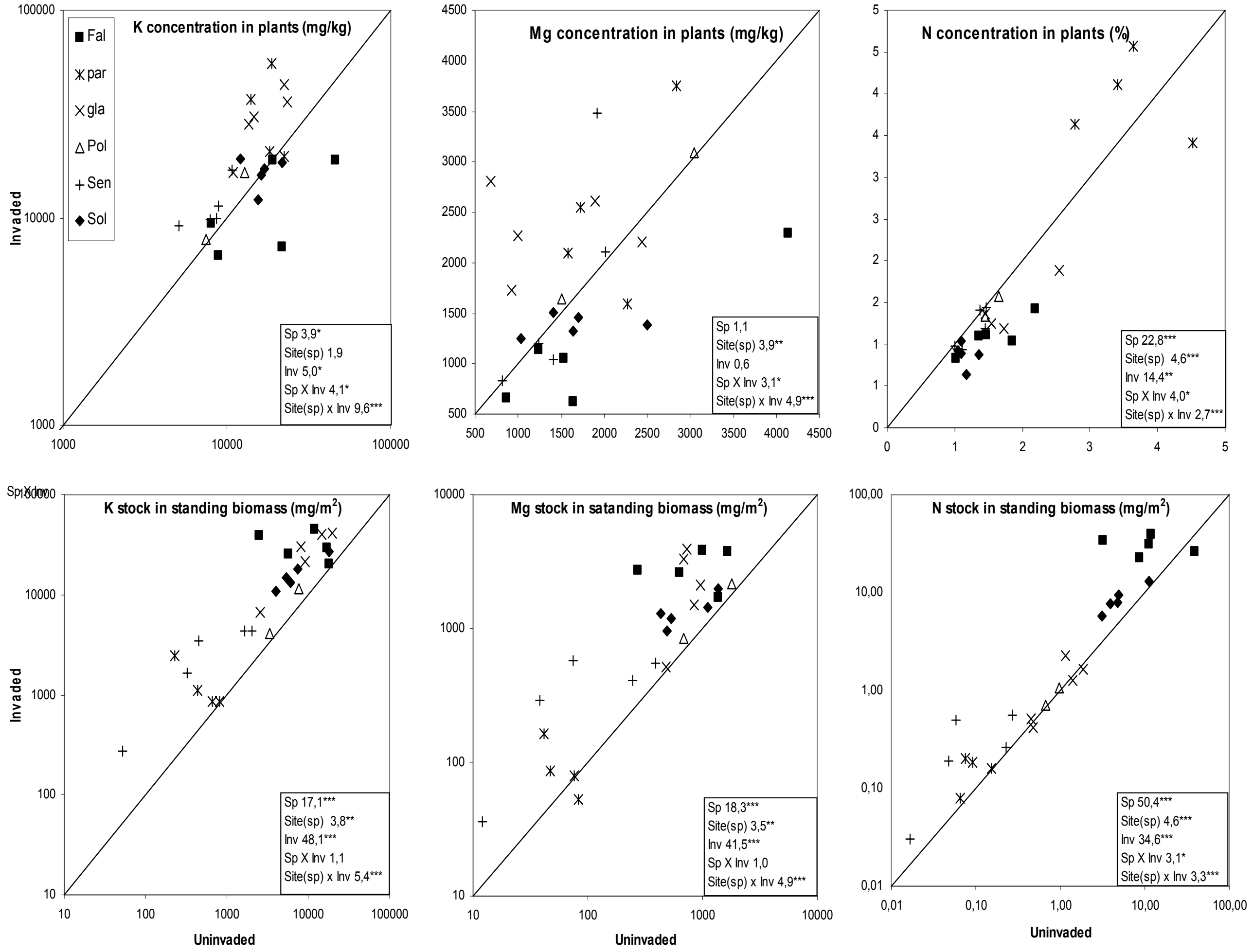


***Figure 14**- K, Mg and N concentrations (mg kg^{-1}) and stocks (mg m^{-2}) in aboveground biomass in invaded and uninvaded plots. The line denotes equal value for invaded and control plots. Value above the line indicates increased value in invaded plot. The results of the three-way ANOVA are indicated: F values and significance level: * P < 0.05; ** P < 0.01; *** P < 0.001.*

◆ S gigantea, ■ F. japonica, ✳ I. parviflora, X I. glandulifera, △ P. caeruleum, + S. inaequidens.

For N, Cu and Mn, concentration in invasive plants was nearly always lower than in uninvaded native vegetation (N: Figure 14, Mn: results not shown). For K, Mg, Ca and P, the three-way ANOVA showed a significant species X invasion effect (Figure 14 and results not shown) explained by the contrasting patterns of the different species: while *F. japonica* and *S. gigantea* had lower concentrations than native vegetation, Both *Impatiens* species showed a higher concentration in K, Mg and, to a lesser extent, Ca and P than the indigenous vegetation. Zn concentration was nearly always higher in invasive plants than in uninvaded native vegetation except for *F. japonica*.

Due to much higher biomass, nutrient stocks were higher in invaded compared to uninvaded plots, for nearly all elements in all species with only few exceptions (Figure 14). However, the magnitude of the increase was variable according to element and to species. The increase was more pronounced for cations and less for

Nitrogen. The three-way ANOVA showed a significant species X invasion effect for N, the increase was indeed clear for *F. japonica* and *S. inaequidens* while it was weak or null for *P. caeruleum* and *I. glandulifera*.

3 Discussion

We have gathered the largest data set documenting impacts of alien invasive plant species on ecosystems in Europe. Nine species have been considered, each with two to six sites, i.e. a total of 42 invasion events, spanning a broad range of vegetation and soil types.

3.1 Alien invasive species increase net primary productivity

With only few exceptions, invasion increases aboveground net primary productivity. Higher net primary productivity and faster growth rates have often been reported in comparisons between invaded and native vegetation (Ehrenfeld 2003; Ehrenfeld *et al.* 2001; Blank & Young 2002). The magnitude of the increase is strongly species-dependent (*F. japonica>>S. gigantea>I. glandulifera>S. inaequidens>I. parviflora*). Two distinct mechanisms can be identified. First, three alien invasive species have higher shoots and faster growth rate compared to the resident vegetation (*F. japonica, I. glandulifera, S. gigantea*). Secondly, *S. inaequidens* and *I. parviflora* invade habitats with sparse ground layer and achieve higher population density and ground cover compared to the resident vegetation.

The most striking productivity increase was found in *F. japonica* (up to 13-fold in site “Ghi”). This species is a shrub-like geophyte, i.e. a growth form which does not exist in the European native flora. It may achieve higher production in a very short period due to mobilisation of large amounts of nutrients and carbohydrates stored in belowground organs (Price *et al.* 2001). *F. japonica* may tap nutrients and water from larger pools compared to the resident vegetation due to deeper rooting depth (up to 2 meter (Child *et al.* 2001)). However, it is not obvious that primary productivity of resident vegetation in sites invaded by *F. japonica* is currently limited by nutrients and/or water.

The increase in net primary productivity most likely has dramatic consequences on ecosystem processes which have not been measured here. alien invasive species certainly enhance carbon fluxes entering ecosystems and fluxes of dead plant organic matter onto the soil. Evapotranspiration flux is most likely enhanced as well. Increased standing biomass certainly results in lower light intensity at ground level (see Section 1). The ability to decrease light intensity may be a key attribute enabling successful alien invasive species to rapidly achieve dominance in invaded ecosystems. Finally, enhanced productivity may also hold true for belowground organs, and may be another key trait enhancing competitive ability of alien invasive species for nutrients.

3.2 Concentrations of nutrients in shoots: two different nutrient use strategies

For some elements and especially N, mineral nutrient concentrations of alien invasive species are lower compared to the resident vegetation. This is apparently at odds with published results showing higher concentrations of nutrients in several invasive species (Baruch & Goldstein 1999; Ehrenfeld *et al.* 2001; Blank & Young 2002). This may be explained by the fact that our data refer to whole shoots, while most published papers have analysed foliar concentrations only.

For some other elements, especially K and Mg, the pattern is species-dependent with two possible situations.

- Certain invasive species such as *F. japonica* and *S. gigantea* have lower nutrient concentrations in their tissues than the uninvaded native vegetation. These species may have higher biomass allocation to nutrient-poor stems. This hypothesis has been verified for *F. japonica*. This species allocates approximately 68% of its aerial biomass to stems poor in Mg (590 mg kg^{-1}), Mn (25 mg kg^{-1}) and to a lesser extent in P (1489 mg kg^{-1}), Zn (27 mg kg^{-1}) and N (0.6%) compared to the 32% of the biomass invested in nutrient-rich leaves (Mg: 5264 mg kg^{-1}, Mn: 263 mg kg^{-1}, P: 2518 mg kg^{-1}, Zn: 54 mg kg^{-1} and N: 2.6%) (Dassonville, unpubl. data).

A key trait of some of the most successful alien invasive species may be the ability to quickly build up high, nutrient-poor stems. If nutrient use efficiency is assessed as the amount of nutrients required to construct 1 g shoot, *F. japonica* is arguably more efficient than the native vegetation.

- Some other species such as *I. glandulifera* and *I.* parviflora apparently have a different nutrient use strategy, since *I. glandulifera* often had higher concentrations of K compared to the resident vegetation. This is in line with the fact that tissue turgescence is the main mechanism ensuring shoot rigidity in this species with low dry matter content (Andrews *et al.* 2005).

3.3 Alien invasive species increase nutrient standing stocks in the plant community

A striking finding is the elevated nutrient stocks in the aboveground biomass of alien invasive species. This is mostly due to increased productivity. In *F. japonica*, low shoot nutrient concentrations are overcompensated for by much higher productivity. In some species, higher tissue nutrient concentrations also contribute to higher nutrient stocks (e.g. K in *I. glandulifera*).

In annual species (*I. glandulifera*) high nutrient standing stocks certainly result in increased nutrient returns in litterfall. In perennial species, this may hold true, except if alien invasive species had considerably higher nutrient resorption from senescing shoots compared to native vegetation, which seems unlikely. It thus appears that alien invasive species steadily enhance specific components of nutrient cycling, including net uptake rate from soil and annual returns in dead organic matter. For those elements that do not rely on mineralization to become available to plant roots (i.e. most elements except N, P and, to a lesser extent Ca), the whole cycle may be enhanced by alien invasive species. This may hold true for N, P and Ca except if microbial activity of humus is strongly depressed under the canopy of alien invasive species, which our results on C and N content in soil generally do not support. We, indeed, rarely showed a significant increase of organic carbon or an increase of C/N ratio in the soil, two indicator of humus activity depression.

3.4 Impacts on soil are species-dependent

When all sites and species are pooled, there is a general tendency for increased concentrations of nutrients in topsoil under alien invasive species, and this is significant for K, Mg and Mn. This result is in line with the published literature on impacts of alien invasive species, in which increased nutrients were much more often reported than decreased nutrients (Musil 1993; Scott *et al.* 2001; Ehrenfeld *et al.* 2001; Ehrenfeld 2003; Vanderhoeven *et al.* 2005; Chapuis-Lardy *et al.* in press but see Belnap & Philips 2001). Nitrogen stands out as an interesting exception.

However, the pattern of impacts on topsoil chemistry is markedly species-specific. The 9 species can schematically be ascribed to one of the three following patterns. Increased concentrations of most nutrients in topsoil were found only for *F. japonica*. In contrast, only little impact on topsoil chemistry was detected for *H. mantegazzianum* and *P. caeruleum*. The third pattern consists of elevations of a single or only few nutrients (P in *S. gigantea*, Ca in *P. serotina*, K, Mg and N in *R. rugosa*, K and Mg in *S. inaequidens*, Mg in *I. glandulifera*, Ca, Mg and P in *I. parviflora*).

3.5 Increased nutrients in topsoil under F. japonica

The most striking impacts on soil were found for *F. japonica*, with 35% to 60% higher topsoil concentrations of Cu, K, Mg, Mn, P and Zn. At some sites, even larger impacts have been found (e.g. 2-fold increase in K and P at Ghi; 2.5-fold increase in Zn and Cu at EN). Large impacts on topsoil chemistry have been well documented for trees (e.g. Musil 1993; Finzi *et al.* 1998a, b; Augusto *et al.* 2002; Hagen-Thorn *et al.* 2004) but seem more unusual for herbaceous species. Only few herbaceous invasive species have been found to have strong impacts on cations and phosphorus bioavailability (Blank & Young 2002; Duda *et al.* 2003; Vanderhoeven *et al.* 2005; Chapuis-Lardy *et al.* in press). For instance, K, Mg and Ca were 3 to 6 times more abundant in the soil solution of soils invaded by *Lepidium latifolium* (Blank & Young 2002). Most of the time, the invasion has an important impact on few elements. To our knowledge, our study is one of the first to demonstrate large impacts of a herbaceous invasive species on many elements in a relatively large number of sites.

Pre-existing variation and plant-driven variation in soil conditions are two mutually non exclusive explanations for these results. The first explanation requires that pre-existing variation in soil conditions is governing the fine-scale distribution *of F. japonica* within all sites. This seems unlikely, for the following reasons. First, the sampling protocol was specifically designed to reduce the possibility of pre-existing differences. Secondly, *F. japonica* is still expanding in most selected sites, and uninvaded plots were located close to the front of expansion of invaded stands. Thirdly, within site variation in soil conditions is always much narrower than the range of soil conditions encompassed by *F. japonica* across sites. In a formal sense, impacts of plants on soil conditions can be formally proven only if time variation in soil conditions following invasion is demonstrated. However, most published studies demonstrating impacts of plant invasions have been performed at a single sampling date (Asner & Beatty 1996; Ehrenfeld *et al.* 2001; Blank & Young 2002; Duda *et al.* 2003; Standish *et al.* 2004).

3.6 Impacts are site-specific; evidence for homogenization effects in Fallopia

The same species can have somewhat different impacts depending on site, a point that has already been made by others (Scott *et al.* 2001; Ehrenfeld 2003). Variation in impacts of *F. japonica* across sites apparently follows a clear pattern. Thus, in contrast to the general trends, sites with the highest values of any particular element in uninvaded plots systematically show decreased values of that element in invaded plots. This holds true for Cu (Har), K (For), Mg (For), P (For), Zn (Har), N (For) and organic matter (Ghi). pH and Mn are the only exceptions to that pattern. In contrast, those sites with the lowermost values in uninvaded plots systematically show increased values in invaded plots (pH: VK, Cu: Gbx; K: VK; Mg: VK; P: all sites except For; Zn: Gbx; N: Gbx; organic matter: Gbx; C/N: Gbx). This pattern can be interpreted as a convergence of invaded plots towards similar values of soil parameters. It is striking that variation range of element concentrations across sites was systematically narrower in invaded plots than in uninvaded ones, most strikingly so for Cu (6.8-fold variation among resident plots vs. 2.4-fold in invaded plots); K (4.1-fold vs. 2.6-fold), P (33.6-fold vs. 10.8-fold), Zn (7.6-fold vs. 2.7-fold), N (2.7-fold vs. 1.5-fold), C (3.7-fold vs. 1.8-fold).

There is also some evidence for homogenization effects when all sites and species are pooled. Thus, soil nitrogen is increased by alien invasive species in those 8 sites with the lowermost initial N concentrations, while it is decreased in those 9 sites with the highest initial N concentrations. It has been proposed that alien invasive species may result in floristic homogenisation of landscapes (Olden & Poff 2003; McKinney 2004). To our knowledge, the present study is the first to provide some evidence for such homogenising effects on soil conditions.

3.7 Mechanisms of impacts of alien invasive species on soil

- Enhanced nutrient uptake rates by *Fallopia japonica*

Plant-driven alterations of topsoil chemical composition can be due to changes in mineral nutrient fluxes in the plant-soil system (Ehrenfeld *et al.* 2001; Blank & Young 2002). Increased nutrient concentrations in topsoil fits in well with our finding of enhanced mineral nutrient cycling rates in invaded plots. In *Lepidium latifolium*, increased topsoil concentrations of several nutrients could be ascribed to correspondingly higher concentrations of these nutrients in tissues (Blank & Young 2002; Duda *et al.* 2003). However, mineral element composition of debris cannot in itself explain increased nutrient pools in topsoil because *F. japonica* has lower tissue nutrients concentrations. However, low tissue concentrations are overcompensated for by 3- to 13-fold higher aboveground biomass production.

Due to resorption from senescing leaves and stems, nutrient returns in litterfall are most likely smaller than annual nutrient allocation for shoot construction. However, this holds true for both invaded and uninvaded stands. Therefore, it is safe to conclude that the amounts of nutrients returned annually to soil in litterfall are much higher in plots invaded by *F. japonica* compared to the resident vegetation. According to Prescott (2002), total nutrient returns via litter fall is the best predictor (better than litter chemistry, e.g. C/N, lignin/N) of the effect of a plant species on nutrient availability in the soil. Enhanced fluxes of nutrients may thus result in increased availability of the corresponding nutrients in topsoil, by the mechanism of nutrient uplift (Jobbagy & Jackson 2004). Thus, if *F. japonica* obtains a significant proportion of mineral nutrients from deeper soil layers compared to the resident vegetation, biogeochemical cycling of nutrients will result in net displacement of nutrients from deep layers to topsoil. *F. japonica* does indeed have very deep rooting depth (at least 2 m: Child *et al.* 2001). Ca pumping from deep soil has also been invoked to explain elevations of Ca under the canopy of the invasive herbaceous *Lepidium latifolium* (Blank & Young 2002).

Interestingly, nitrogen does not follow the same pattern as metallic elements. Thus, in spite of a general increase in N stocks in standing biomass of alien invasive species, N is not generally increased in topsoil most likely because uplift is not possible for an element that is mostly concentrated in the upper soil layers.

- Mobilisation of soil P by *Solidago gigantea*

In spite of higher nutrient stocks in standing phytomass, there was no general increase in mineral nutrients in topsoil under *S. gigantea*. Phosphorus stands out as a notable exception, with 70% higher concentrations. Nutrient uplift from deep soil layers cannot explain elevation of only a single nutrient. Moreover, *S. gigantea* does not seem to root considerably deeper than resident vegetation with 85% of the belowground biomass concentrated in the upper 6 cm vs. 80% for the resident vegetation (Dassonville *et al.* unpubl. obs.). An alternative hypothesis is that soil P availability *is* altered by *S. gigantea* (Notice that soil P measured in this paper represents extractable, not total, P). Recently, Chapuis *et al.* (2005) found increased pools of labile P in soil under *S. gigantea*. These were correlated to increased activities of phosphomonoesterase and increased soil respiration rate. Thus, enhanced P mineralization rates may well be involved in the increased pools of bioavailable P in the topsoil. *S. gigantea* may also be able to use P pools that are less available for plants compared to the surrounding vegetation. This could be the consequence of mycorrhizal processes, which have been documented for the closely related invasive *S. canadensis* (Jin *et al.* 2004). Topsoil labile P pools may also be increased as a result of increased effluxes of H^+ or exudation of organic acids by roots (Hinsinger 2001). Significant acidification under *S. gigantea* compared to uninvaded plots supports the latter hypothesis.

SECTION 3: PATTERNS AND PROCESSES OF INVASION AT THE LANDSCAPE SCALE

A MONITORING OF SPECIES AND ANALYSIS OF DISPERSAL-SPREADING AT THE LANDSCAPE LEVEL

1. Material and methods

1.1 Seed dispersal cycle

Seed dispersal cycle was analysed for four target invasive species: *Senecio inaequidens*, *Fallopia* spp., *Heracleum mantegazzianum* and *Prunus serotina*. The methodology was adapted to the reproduction type and ecology of each species. For *S. inaequidens* and *H. mantegazzianum*, two anemochorous species, data were collected in two populations with contrasting adult densities : PA (51°14'37.4''N; 04°23'12.3''E) and PS (50°36'9.1''N; 05°29'46.0''E) for *S. inaequidens*, VEN (50°47'31.2''N; 04°24'29.9''E) and MG (50°37'20.3''N; 04°42'43.2''E) for *H. mantegazzianum*. For *Fallopia* spp., expected to reproduce essentially by vegetative means (Beerling *et al.* 1994), 9 clones were selected in the vicinity of Gembloux. For *P. serotina*, that produces fleshy fruits dispersed by birds, data were collected in the Meerdael forest.

Seed production by plant (individual or clone) was estimated by multiplying the mean number of seeds produced per capitulae (*S. inaequidens*, n=10/individual), umbel (*H. mantegazzianum*, n=1/individual) or stem (*Fallopia* spp.: n=3/clone, *P. serotina* : n=5-25%) by the total number of capitulae, umbels or estimated number of stems per plant (*S. inaequidens*: n=10, *H. mantegazzianum*: n=5), clone (*Fallopia* spp.: n=9) or tree (*P. serotina:* n=6).

Seed quality was assessed by germination tests in laboratory in Petri dishes, without stratification (incubation chamber: temperature min. 15° C/max. 20 °C, photoperiod 16 h) and with stratification (4°C, no light, *S. inaequidens*: 15 weeks, *H. mantegazzianum*: 6 -15 weeks, *Fallopia* spp.: 0-15 weeks, *P. serotina*: 0 -17 weeks).

Seed rain of *S. inaequidens* and *H. mantegazzianum* was assessed using 10 cm diameter seed traps situated on the centre of 1x1m quadrats arranged along linear transects (1 transect with 40 seed traps in each *S. inaequidens* population; 25 and 45 seed traps in MG and VEN, respectively, for *H. mantegazianum*). For *P. serotina*, 62 seed traps (diameter: 10 cm, height: 5 cm), were arranged on a 10 x 10m grid.

Seed bank of *S. inaequidens*, *H. mantegazianum* and *Fallopia* spp. was estimated in autumn and spring by the seedlings emergence method (Bakker *et al.*, 1996). *For S. inaequidens* and *H. mantegazianum,* samples were collected in the quadrats used for seed rain quantification. Three bulked soil cores (4 cm diameter x 10 cm depth) were collected in each quadrat. For *Fallopia* spp., 5 soils cores (4 cm diameter x 5 cm depth) were sampled under canopy of 14 clones (n=5/clone). Samples were separated in layers according to soil depth (litter, 0-5 cm and 5-10 cm), dried at 20°C, sieved through a 2 mm mesh sieve and poured on germination trays for germination at a temperature of 20°C and a light period of 16 hours to quantify seed bank.

1.2 Dispersal capacity

Detailed studies of dispersal capacity of seeds were undertaken for two of the target species with contrasting seed vectors : *S.inaequidens* (wind dispersed) and *P. serotina* (bird dispersed).

***Senecio inaequidens*.** The data collected for the seed cycle description along transects in the two populations were used to detect spatial pattern linked to limited spatial seed dispersal. First, spatial dependency among adult density, seed rain, autumn seed bank and winter seed bank were tested with Spearman correlations (between successive stages in the cycle) using quadrats as repetition. In order to analyze the spatial structure of the different stage, spatial autocorrelation statistics were applied using Moran's I coefficient (Dark, 2004). Seed dispersal capacity, and its variation, was further analysed in controlled conditions. In anemochorous species, terminal velocity has been shown to be a good predictor (proxi-trait) of mean seed dispersal distance in non turbulent air flow. In both populations, five capitulae were randomly collected on each of five randomly selected individuals. On each capitulae five external achenes (at the periphery of the receptacle) and five internal ones (near the centre of the receptacle) were randomly picked and measured. Terminal velocity was measured as the drop time in still air in a plexiglas tube with three replicate measures per seeds (N=100). Linear regression using multiple least-square estimation was used to model terminal velocity by seed morphological traits. Differences for those morphological traits that explained the variation of terminal velocity were analysed using nested ANOVA with position (central or periphery) nested in capitulae, capitulae nested in individuals and individuals nested in population, all of them being random factors. Additional dispersion experiments were conducted in a low-speed wind tunnel, using entire infructescence, with a wind speed of 5m/sec and turbulences reaching about 7%, 2%, 3% of the wind speed respectively vertically (Y axis), normally (Z axis) and in the wind direction (X axis). The ground was covered with a six-meterlong adhesive paper reaching the end of the test section of the tunnel. The bottom of the test section (at the opposite of the blowing engine) was covered with a vertical textile collector which allowed achene fixation. After each dispersion event, achenes were collected for the same morphological measurements as above after their distance from the capitulum on the adhesive paper, or their height on the vertical collector, were taken. Propagules that were vertically collected above 0.40 m were considered as uplifted. Besides morphological measurements, clustered and aborted aspect were noted for each achene (binary characteristic).

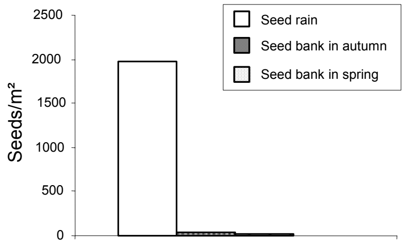
Prunus serotina. In the population used for seed rain quantification, *P. serotina* adult trees (n=300) were plotted and their circumference at breast height (CBH) measured. Fruits were collected in seed trap (n=62, grid 10x10 m) weekly and separated in fruits with mesocarp and without mesocarp (regurgitated by birds). Inverse modeling approach described by Ribbens *et al*. (1994) was used to identify the specific source location of dispersed seeds. Three dispersal functions for trees (the weibull probability function (Ribbens *et al*. 1994; Clark *et al*. 1998; Clark *et al*. 1999), the 2Dt (Clark *et al*. 1999) and the lognormal (Greene and Johnson, 1989) were compared.

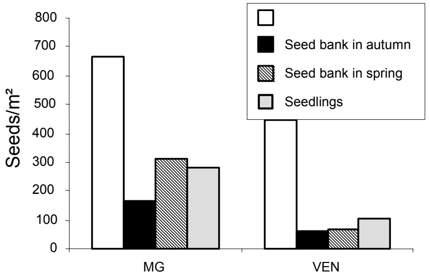
1.3 Landscape structure influence on distribution and dynamics of populations

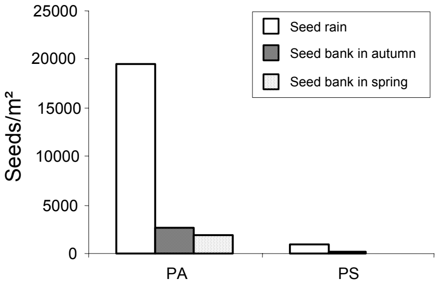
Two landscape units (LU), Comblain (Co : 50°28’8.95’’N; 05°34’29.8’’E; area: 1006.7 ha) and Kessel (Ke: 51°8’7.34’’N; 04°37’11,29’’E; area: 987.3 ha) about 1000 ha each, were prospected during the flowering period 2003 to map all populations of invasive target species : *Fallopia* spp., *H. mantegazzianum*, *I. glandulifera*, *S. inaequidens* and *Solidago gigantea / S. canadensis*. Population localization was reported on 1/10.000 topographical maps with the help of GPS coordinates. For each LU, the structure of the landscape (habitat composition and spatial configuration) was characterized on the basis of recent land use cover map (IGN TOP10V-GIS) with a GIS (ESRI, Arcview 3.2). Habitat selection was assessed for each target species with a selection index (SI) : $S_i = [(n_i/N)/(S_i/S)]$ where n = number of populations in the *i*th habitat, N = total number of populations in the landscape unit, S_i = total surface of the *i*th habitat in the LU, S = landscape unit area (adapted from Manly *et al.*, 1993). In addition, on the field, we noted when the population was present in a microhabitat embedded in the general land use class using the following classes : river bank, hedgerow, pavement, wall, filled in area. The structure of each landscape was assessed on the basis of 1) its global level of fragmentation (number of patches and mean patch size) and 2) the patch structural characteristics of each habitat (size : area; shape : perimeter to area ratio; isolation : distance to the nearest neighbour and connectivity index (Higgins *et al.*, 1999; Winfree, 2005). The influence of the landscape structure on the pattern of distribution of the target species population was assessed by logit regression of presence(0)/absence(1) of the species in a patch (dependent variables) on the patch structural characteristics (independent variables) for area, nearest neighbour and connectivity indexlog transformed. The influence of linear networks (landscape corridors) on target species distribution was analysed by estimating the proportions of populations situated within buffers of 5, 10 and 50 m around rivers, roads and railway networks. The spreading dynamics of each species was assessed on the basis of a second survey of Ke in 2005. Recently colonizing populations (<2y) were identified by comparison with the survey of 2003. To examine the influence of the landscape structure on the spreading pattern of each species, the same analysis of habitat selection, patch structure influence and linear networks were realized on the recent populations.

F. japonica

Seed demography

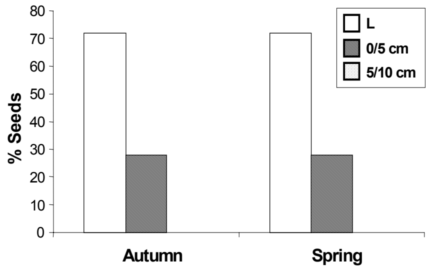


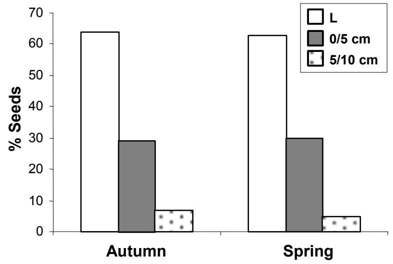




Vertical distribution
Seed bank

No seed bank





Germination **rate**

60 ± 34% for fresh seeds
10 ± 10% after stratification

0% for fresh seeds
From 1,6 ± 2,6 % to 62 ± 22% according to the stratification period

88 ± 13 % for fresh seeds
36 ± 6 % after stratification

Decrease of germination and seed viability after stratification

Need stratification
LOST OF SEED VIABILITY AFTER SEED DRYING

STRATIFICATION REDUCED SEED GERMINATION POTENTIAL

Figure 15. Results of the different seed flow steps obtained for *Fallopia* spp., *H. mantegazzianum* and *S. inaequidens*. L: Soil litter, 0/5 cm: soil portion from surface to 5 cm deep, 5/10 cm: soil portion from 5 to 10 cm deep.

2. Results

2.1 Seed dispersal cycle

Seed production per plant (Figure 15): For *S. inaequidens*, the flowering period extended from July to January. Two flowering peaks were observed: July and October. The relative importance of the flowering peaks differed between populations with a maximum of flowering in July for PS and in October for PA. A plant of *S. inaequidens* produced on average 34774 ± 13285 seeds in PA and 22617 ± 5799 seeds in PS (difference not significant). For *H. mantegazzianum*, a plant produced on average 9468 ± 6283 seeds in MG and 11062 ± 11803 seeds in VEN difference (not significant). For *Fallopia* spp., a clone produced on average 424597 ± 410789 seeds. The mean observed total fruit production per *P. serotina* tree was 3372 ± 1049 and 21 % of this production was eaten by birds (disappeared mesocarp).

Seed rain (Figure 5)**: -** In the *S. inaequidens* populations, seed rain reached on average 19481 ± 23952 seeds/m² in PA (10 ± 9 plants/m²) for 920 ± 1509 seeds/m² in PS (2 ± 5 plants/m²; $P<0,001$). For *H. mantegazzianum*, mean seed rain reached 668 ± 1105 seeds/m² in MG (2 ± 0,9 plants/m²))for 443 ± 896 seeds/m² in VEN (3 ± 2 plants/m²; difference not significant). Under a *Fallopia* spp. clone, seed rain reached on average 1974 ± 1133 seed/m² (49,6 stems/m²). In the *P. serotina* sampled population, mean seed rain reached 272 and 64 seeds/m² (1 tree/m²) respectively for fruits with and without mesocarp.

Seed bank (Figure 15)*:* In the *S. inaequidens* populations, the size of the seed bank in autumn was 2653 ± 4826 seeds/m² in PA for 119 ± 360 seeds/m² in PS (significantly different: $P=0,001$). As compared to autumn, the size of the spring seed bank was decreased by 29% in PA (1881 ± 1892 seeds/m²) and 39% in PS (72 ± 173 seeds/m²). In the two populations, the density of the seed bank decreased with increasing soil depth with a very similar pattern. About 60% of seeds were found in the litter in both sampling periods. However, a significant number of seeds were found in the 5-10 cm soil layer indicating that the seed bank of *S. inaequidens* should be classified as short term persistent. For *H. mantegazzianum*, the size of the seed bank in autumn was 167 ± 346 seeds/m² in MG for 60 ± 175 seeds/m² in VEN (difference not significant). Seed bank in spring (before spring germination on the field) reached on average 312 ± 416 seeds/m² in MG for 73 ± 147 seeds/m² in VEN ($P<0,001$). Spring seedlings density was very similar to spring seed bank density. More than 70 % of the seeds were located in the litter and no seeds were found in the deeper soil layers indicating that the seed bank of *H. mantegazianum* should be classified as transient. For *Fallopia* spp., the size of the seed bank was 227 ± 58 seeds/m² in autumn and 34 ± 92 seeds/m² in spring. All seedlings were found in the litter. *Fallopia* spp. consequently did not form persistent seed bank.

Mean germination rate of fresh seeds of *S. inaequidens* was 88 ± 13 % as compared to 36 ± 6% for stratified seeds. Stratified seeds of *H. mantegazzianum* germinated on average from 1,6 ± 2,6 % to 62 ± 22 % according to stratification duration (6 and 23 weeks respectively) whereas fresh seeds did not germinate at all. For *Fallopia* spp., mean germination rate of fresh seeds was 60 ± 34 % as compared to 10 ± 10 % for stratified seeds. Fresh seeds of *P. serotina* did not germinate, stratified seeds germinated on average at 30 ± 3,4 %.

Dispersal capacity

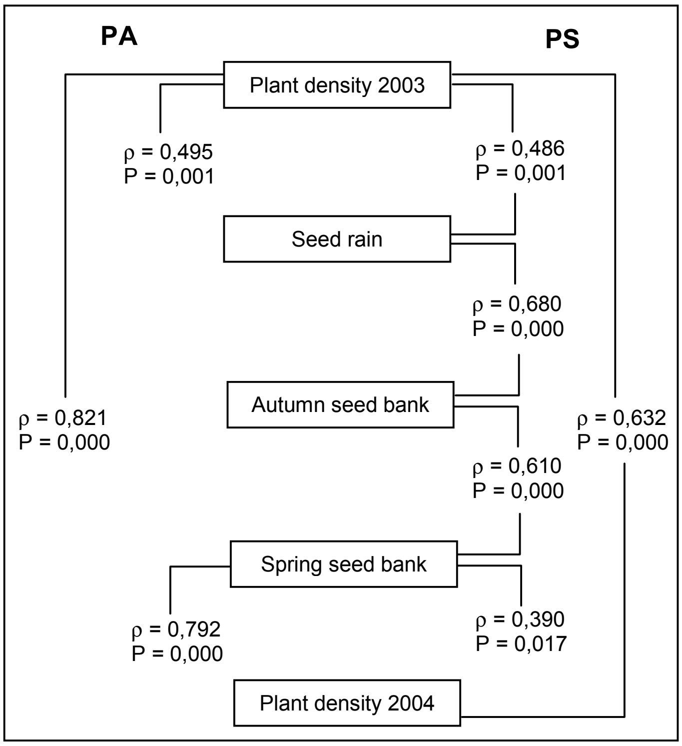


***Figure 16**. Correlations between the seed flow steps in two populations of Senecio inaequidens, PA: population in Antwerp, PS: population in Seraing.*

***Senecio inaequidens**.* The seed flow steps were all positively correlated in PS. For PA, plants densities in 2003 and 2004 were positively correlated, like the plant density in 2003 and the seed rain, the seed bank in spring and the plant density in 2004 (Figure 16). Significant autocorrelations were found for all stages in the first class of distance (0/2 m) in PS and the first two classes of distances (0/4 m) for PA (Figure 17), except for the seed bank in spring.

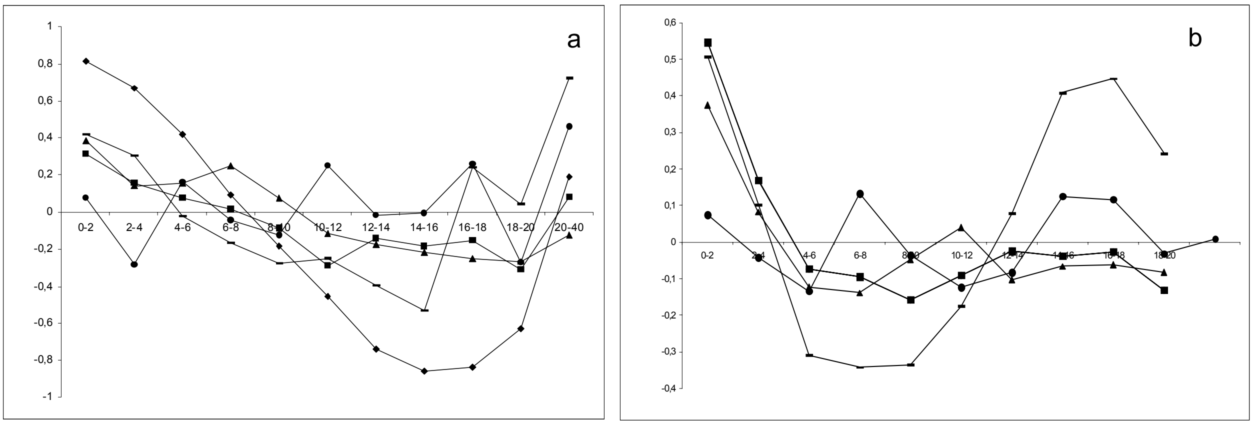


***Figure 17** - Spatial autocorrelation in the Senecio inaequidens population located in: a, Antwerp; b, Seraing (I Moran). ♦ : Density in 2003, ■: Seed rain, ▲: Seed bank in autumn, ●: Seed bank in spring, - :Density 2004.*

The shapes of the autocorrelograms of the different stages were very similar in each population and may be interpreted as an indication of patchy distribution. Patchy distribution coupled to spatial dependency of the different stages may be caused by limited seed dispersal within sites, with most seeds being dispersed in the close vicinity (0/4 m) of the parents. The most correlated quantitative morphological trait (out of 30) with terminal velocity was the square root of plume loading (r = 0.901; $P <$ 0.001), that alone explained 81.3% of the terminal velocity variability. No difference was found between populations nor any morphological trait nor terminal velocity. A great part oof the variability in morphological traits was explained either by individuals, capitulae and position of the achene on the receptacle. Terminal velocities of the 219 propagules dispersed and measured in the wind tunnel experiment was estimated from morphological characters using the regression model described above. Primarily, assuming the homogeneity of the air flux in the windtunnel, the theoretical dispersion distance of each non-uplifted propagule was calculated considering its theoretical terminal velocity (using the model described above) and the constant wind speed. Under this hypothesis, we besides determined the dispersion distance of the 76 propagules that were attached to the vertical collector under 0.4 m (no uplift) by linear extrapolation over 6 m. Indeed, in laminary air flux, the fall of the achene-pappus unit would be constant. Thus, each of the 197 non-uplifted achene-pappus units was linked to a theoretical (modelled) and an actual (either directly measured or extrapolated) dispersion distance. These two dispersion distances were found not to be correlated (r = 0.09; P = 0.261), which indicates that wind homogeneity was not an appropriate hypothesis and extrapolation was wrongful. This was thus repeated considering only propagules dispersed under 6m (no extrapolation) but again no significant correlation was found (r = 0.076; P = 0.452). Dispersion along the tunnel can thus not be modelled using terminal velocity of the propagules, because of the heterogeneity of the air flux. Despite rather low turbulence values, 7.8% of propagules uplifted because of turbulences and convection along the tunnel test section. Comparing uplifted and non-uplifted achene-pappus units, we found significant effects of several morphological trait, but when aborted propagules were removed from the dataset, the only significant effect was that of the aggregation (*t*-test, n_1= 219 , n_2 = 12, T = -2.84, P = 0.016).

Prunus serotina. The best model of dispersal for the fruits with mesocarp was the lognormal and it predicted that 95 % of the seeds fall 5 m away from the maternal tree. The best model for the fruits without mesocarp was the weibull and these fruits were predicted to fall much farther (Figure 18). 99 % of these fruits were indeed predicted to fall 49 m away from the source tree. Because the fruits without mesocarp only represented 19% of the total seed crop, the main majority of the seed rain falls near the source tree, confirmed by the shape of the curve modeled for the total number of fruits.

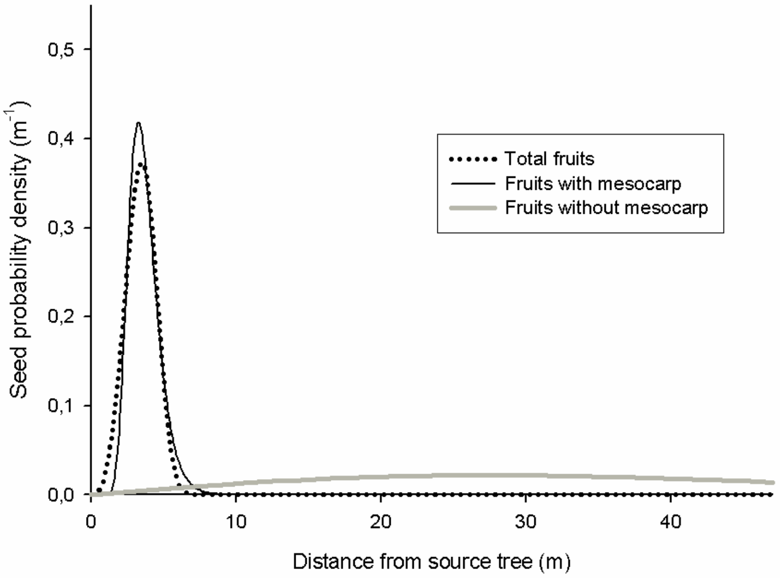


Figure 18 *- Modelisation of Prunus serotina seed dispersal curve.*

2.2 Landscape structure influence on distribution and dynamics of populations

The two LU exhibited contrasted habitat composition and structure. Co was dominated by agricultural and forest land use classes whereas Ke was dominated by urban land use classes (Figure 19). Habitats were less fragmented in Co than in Ke with 812 (mean size 1,885 ± 4,54 ha) and 1435 (mean size 0,804 ± 2,4) habitat patches, respectively. Urbanized patches were also more grouped in Co (along the main river corridor) than in Ke.

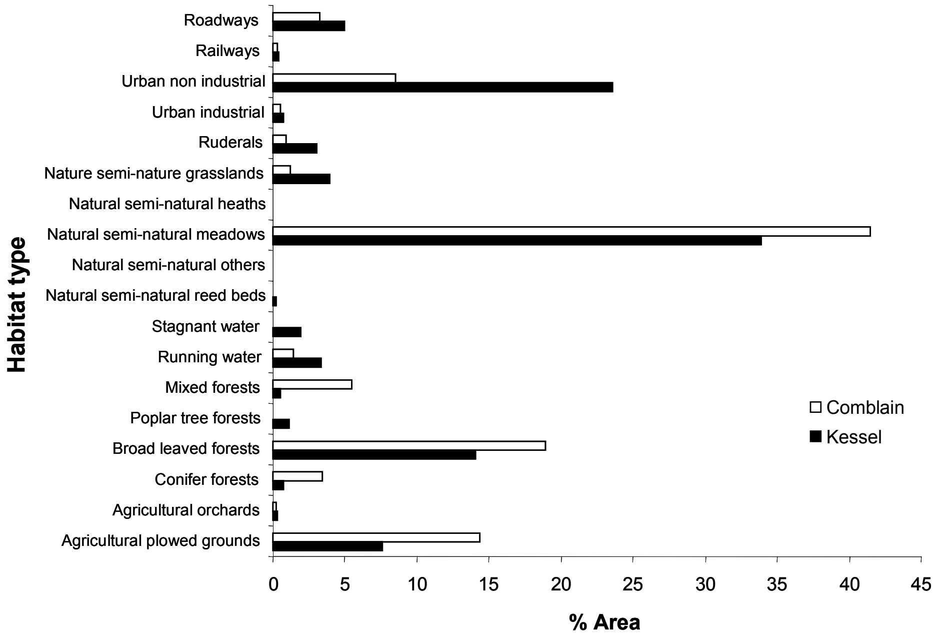


Figure 19 *- Comblain and Kessel land use cover details*

Table 6 - *Habitat selection for the target invasive species populations occuring in the landscape units Comblain (C) and Kessel (K) in 2003. "SI": Selection index (Manly et al., 1993), "Population number": total populations number in the landscape unit, "Density": populations density per ha for the landscape unit. "-": habitat absent in the landscape unit. The shady cells show the habitat selected (SI>1).*

Habitat type	***All species***		***I. glandulifera***		***Fallopia* spp.**		***S. inaequidens***		***S. gigantea/ canadensis***	
	C	**K**	**C**	**K**	**C**	**K**	**C**	**K**	**C**	**K**
Agricultural plowed grounds	0	0,2	0	0,2	0	0	0	0	0	0,6
Agricultural orchards	0	0	0	0	0	0	0	0	0	0
Conifer forests	0	0	0	0	0	0	0	0	0	0
Broad leaved forests	0,9	2,4	0,8	2,5	1,6	2,9	1,5	1,0	0	2,0
Poplar tree forests	0	1,5	0	1,9	0	0	0	0	0	1,7
Mixed forests	0,2	0	0	0	1,1	0	0	0	0	0
Running water	0	0	0	0	0	0	0	0	0	0
Stagnant water	0	0	0	0	0	0	0	0	0	0
Natural semi-natural reed beds	-	2,2	-	3,4	-	0	-	0	-	0
Natural semi-natural others	0	-	0	-	0	-	0	-	0	-
Natural semi-natural meadows	0,1	0,2	0,1	0,2	0,1	0	0,5	0,4	0,5	0
Natural semi-natural heaths	-	0	-	0	-	0	-	0	-	0
Natural semi-natural grasslands	50,4	5,8	61,2	8,1	24,4	3,9	24,4	1,0	23,2	0,4
Ruderals	1,1	1,8	0	1,9	4,1	0	0	2,7	4,5	1,5
Urban industrial	7,8	0,3	5,1	0	11,7	0	16,4	4,4	15,6	0
Urban non industrial	0,7	1,0	0,1	0,5	1,7	1,7	1,1	2,2	4,1	2,4
Railways	0	0	0	0	0	0	0	0	0	0
Roadways	0	0	0	0	0	0	0	0	0	0
Populations number	358	340	255	220	70	35	10	22	21	61
Populations density	0,356	0,344	0,253	0,223	0,070	0,035	0,010	0,022	0,021	0,062

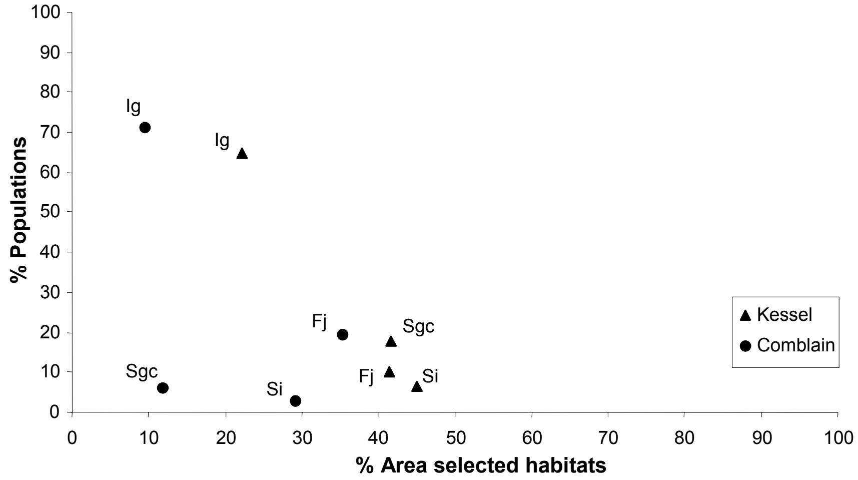


***Figure 20**. Relation between invasives species occurences and selected habitats abundance for the landscape unit Kessel. Fj: Fallopia spp., Ig: I. glandulifera, Si: S. inaequidens, Sg: S. gigantea/canadensis.*

In 2003, the population density of all target species together was 0.34 and 0.35 populations/ha in Co and Ke, respectively. In both landscapes, *I. glandulifera* was proportionally the most widespread species followed by *Fallopia* spp. in Co and by *S. gigantea/canadensis* in Ke. *S. inaequidens* was less widespread in both landscapes and *H. mantegazzianum* was very rare (Figure 20). In the LU Comblain, the natural semi-natural grasslands and the urban industrial habitats were the most selected habitats. In the LU Kessel, the natural semi-natural grasslands, the ruderal and urban non industrial habitats were positively selected. When habitats were selected in 2003, selection index was largely superior to 1.0 indicating strong preferences for them (Table 6).

***Table 7** - Increase, mortality and colonization percentages for the period 2003-2005, in the landscape unit Kessel.*

	Fallopia spp.	*H. mantegazzianum*	*I. glandulifera*	*S. inaequidens*	*S. gigantea/ canadensis*	Total
%increase	14	150	82	82	80	71
% mortality	-	50	11	11	20	13
% colonizing	14	200	94	94	100	83

In 2005, in Ke, the number and density of target species populations had increased by 71 % as compared to 2003. This results from a metapopulation dynamic with colonisation rate (83%, new populations in 2005/populations in 2003) far exceeding extinction rates (13%)(Table 7). There was as strong correlation between the number of new populations found in 2005 and the number of populations present in 2003 for each species ($r^2 = 0.97$, $P<0.01$). However, the relative increase in population number between the two sampling dates varied strongly among species with a maximum of 200% increase for H. mantegazianum and a minimum of 14% increase for *F. japonica*. There was no correlation between the increase rate of a species and its initial number of populations in the landscape (r^2 : 0.004, $P = 0.92$).

For the most widespread species (*Fallopia* spp., *I glandulifera*, *Solidago* spp.) most new populations (>80%) found in 2005 colonized habitat selected in 2003. In contrast for the less widespread species (*S. inaequidens* and *H. mantegazianum*) the majority of new populations colonized habitats that were not preferentially selected by the species in 2003. Those results suggest different dynamics of increase among species with species in the initial exponential phase of expansion not having colonized all the favourable habitats and species near to landscape saturation.

Table 8 - *Repartition (%/species) of the new populations appeared in 2005 in the lanscape unit Kessel between the different habitat types. Shady cells show habitat types selected in 2003*

	Fallopia spp.	*I. glandulifera*	*S. inaequidens*	*S. gigantea/ S. canadensis*
Agricultural plowed grounds		3		
Broad leaved forests	40	10	43	11
Natural semi-natural reed beds		3	14	
Natural semi-natural meadows		4		3
Natural semi-natural grasslands		66		5
Ruderals	20	5		2
Urban non industrial	40	9	43	79
Population number	5	206	7	61

Table 9 - *Results of the logit regressions between presence-absence of species and patch characteristics in Comblain and Kessel . ns: no significant, *: 0,01<P<0,05, **: P<0,01. S: area, P: Perimeter, NN: nearest neighbour distance, Winfree: Isolation index (Winfree, 2005), Log: logarithmic transformation.*

		S (log)	P/S	NN (log)	Winfree (log)
Comblain	*Fallopia spp.*	+ **	- *	NS	NS
	I. glandulifera	+ **	NS	NS	+ *
	S. inaequidens	+ **	- **	NS	NS
	S. gigantea/canadensis	+ **	- **	- *	**NS**
Kessel	*Fallopia spp.*	+ **	NS	**NS**	**NS**
	I. glandulifera	+ **	NS	- **	+ **
	S. inaequidens	NS	NS	NS	**NS**
	S. gigantea/canadensis	+ **	NS	NS	+ **

Patch surface influenced significantly the probability of presence of the species in both landscapes, except for *S. inaequidens* in Kessel. The larger the patch, the higher the probability it is colonized by one of the target invasive species. Other patch metrics were less influential on patch presence and when significant relationship was found it was not always consistent among the two landscapes. The shape of the patch influenced significantly the presence of three out of the four species in Comblain but not in Kessel. Patch with a higher proportion of edge (higher perimeter to surface ratio) were less colonized than patch with a lower proportion of edge. Patch connectivity influenced significantly the presence of *Impatiens glandilufera*, with more connected patches more prone to invasion in both landscapes. The same trend was found for *Solidago* spp. In Kessel.

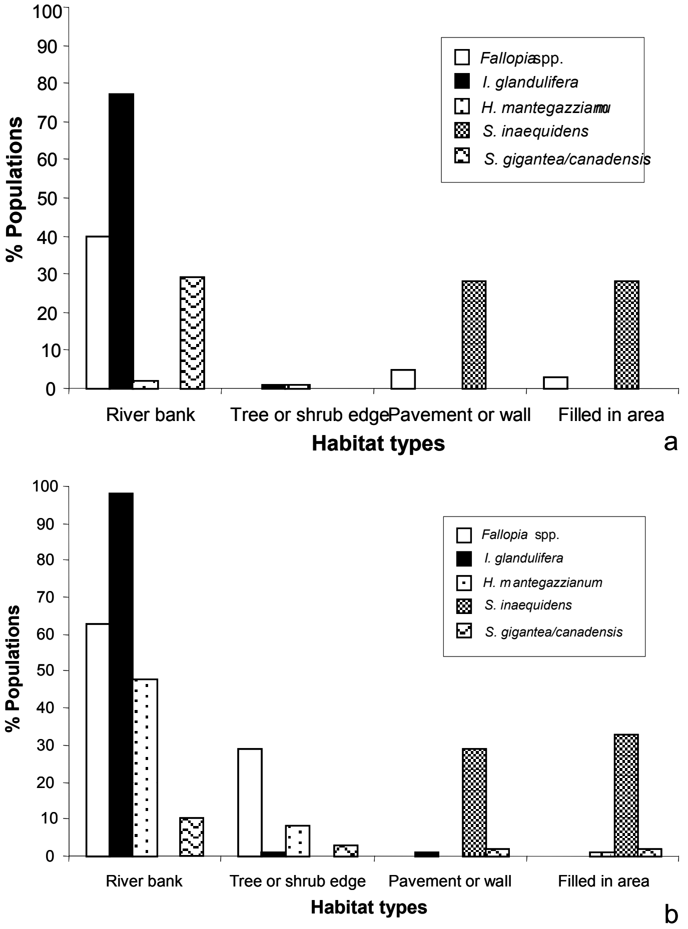


***Figure 21**. Populations distribution (%) in micro-habitats for the selected habitat types in the studied landscape units a: Comblain and b: Kessel in 2003.*

Within the selected habitats, an important proportion of *I. glandulifera* and *Fallopia* spp. populations occurred on river bank microhabitats. Hedgerows were also a significant micro habitat for *Fallopia* spp. in Ke (Figure 21). 55 % and 87 % of the target species populations occurred within a 5 m buffer around linear networks while the area covered by those networks represents only 9 % and 15 % of the Ke and Co respectively. Almost all the populations were situated in a buffer of 50 m around the networks (Figure 22). 74 % of the new populations in 2005 also occurred in a 5 m buffer around networks (Figure 23).

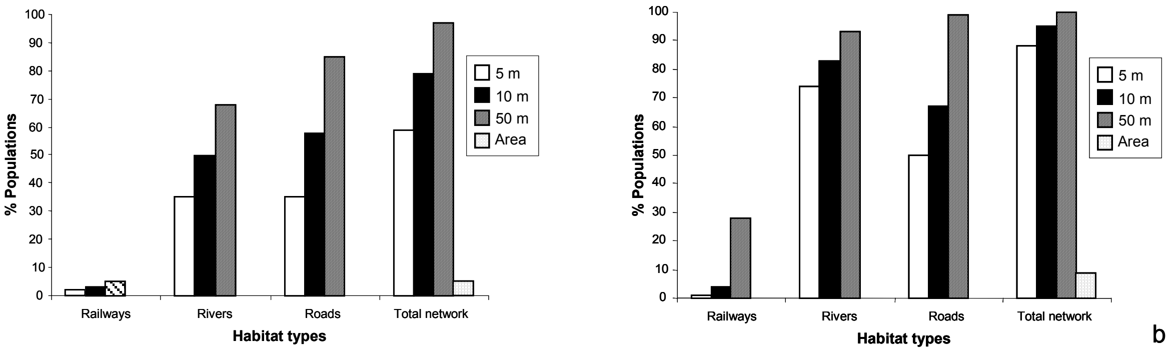


Figure 22 *- Populations repartition (%) in 5, 10 and 50 m buffers around linear networks in the landscape units a: Comblain and b: Kessel in 2003. Area: area proportion covered by the networks in the landscape unit.*

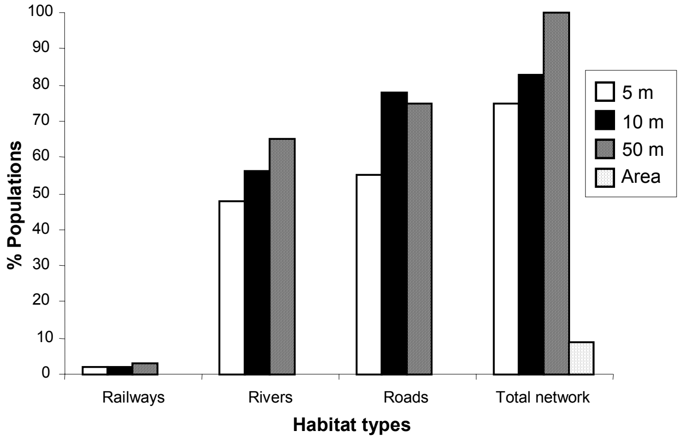


Figure 23 *- New appeared populations repartition around the linear networks in landscape unit Kessel in 2005. Area: area proportion covered by the networks in the landscape unit.*

3. Discussion

3.1 Seed dispersal cycle

Reproductive characteristics are crucial for the invasive success of any alien plant. The present study is the first extensive and detailed description of the seed dispersion cycle for the target invasive species using a similar methodology (but see Krinke *et al.* 2005, for *H. mantegazianum*) and allowing direct comparisons between populations within species or among species. Our estimations of individual seed production for *S. inaequidens*, *H. mantegazianum* and *P.serotina* are within the range described in other studies (Aucair and Cottam, 1970; Ernst, 1998; Forman and Kesseli, 2003; Tiley *et al.*, 1996, but see Krinke *et al.* 2005). All the species examined exhibited high maximum germination rates but differed in stratification requirement. While fresh seeds of *S. inaequidens* and *Fallopia* spp. displayed a better germination success, *H. mantegazzianum* and *P. serotina* seeds need stratification to germinate. Those differences may originate from adaptation to different climates in the native range of the species. Much less is known about seed rain and the formation of seed bank for the selected alien plants, which is an important aspect of seed plant strategies that may favour invasiveness (Krinke *et al.* 2005). In all the species examined we found a high density seed rain but only a small portion of this seed rain build the seed bank. None of the examined species formed long term persistent seed bank (according to Thompson 1993). From our observations, it may be concluded that *H. mantegazianum* forms a transient seed bank with no or extremely low accumulation of seeds over years as proposed by Thompson *et al.* 1997. This is partly in contrast with the study of Krinke *et al.* (2005) who observed a short term persistent seed bank for the species in central Europe. This underlines the necessity of detailed studies in different climatic regions to take life history traits variation into account. The results observed in Belgium suggest that eradication of *H. mantegazianum* population may be achieved by adults eradication followed by a short term monitoring of seedling emergence. We also provide the first quantitative detailed characterisation of the seed bank for *S. inaequidens* in its introduction rain. The species develops short term persistent seed bank. This is especially relevant with respect to control, given that *S. inaequidens* fecundity and high percentage of germination (even a few seeds persisting in the seed bank over years) can potentially start a new invasion.

An important point of this study is the demonstration of the restoration of sexual reproduction due to hybridisation in the male-sterile *Fallopia japonica.*

The restoration of sexual reproduction in F. japonica by hybridization with other species as well as hybrids should considerably allow to generate genotypic diversity, which was lacking in the introduction area (Hollingsworth et al. 1998), increasing the ability of species to adapt in new environments. Moreover, the newly formed genotypes would be fixed by extensive vegetative regeneration. The extensive sexual reproduction by hybridization we observed in the present study definitely contributes to the amazing invasive success of Japanese knotweeds in Belgium and should not be underestimated.

3.2 Seed dispersal capacity.

Our results on seed dispersal in *S. inaequidens* point to the difficulty to accurately model long distance seed dispersal, a key trait to understand invasion patterns. Within populations, spatial autocorrelation at short distance associated to spatial correlation between adult density and seed bank suggest that most seeds are distributed in patch at small distance from the parent source. However, wind tunnel experiments showed that a significant proportion of seeds are uplifted even in the presence of only low level of turbulence. Because, a significant proportion of those uplifted seeds were aborted, the signification of long distance dispersal, due to uplift, for colonisation of new habitat patches is not clear. More advanced techniques are needed to understand the long distance dispersal capacity of the species and to link it to spreading pattern observed in the field.

Results obtained for *P. serotina* showed that in homogeneous forests, even under pine canopy, seeds are in part dispersed by birds, but the majority of the seed crop falls near the parent plant. Therefore, in order to limit the implantation of the species in uninvaded plots, attention must be paid to detect any new seed bearer individual because it can produce massive fruit crops and be a new important seed source within a few years (Pairon *et al.*, 2006).

3.3 Landscape structure influence on population distribution and dynamics.

Assessing the behaviour of invasive species at the landscape level is particularly important from a management perspective because political decisions leading to management strategies will generally concern large geographic area (Higgins *et al.*, 2001). The present study consisted in the first landscape approach for individual invasive plant species. Previous studies focussed on the relationships between landscape structure and exotic species richness (Bruno *et al.*, 2004; Lavoie *et al.*, 2003; Pino *et al.*, 2005; Song *et al.* 2005). However, because we demonstrated that different species present different reproductive and dispersal strategies, a detailed species-based approach is needed to understand the patterns of invasion at the landscape level. In contrast to most previous studies at the landscape scale, we explicitly adopted a comparative approach by assessing the patterns of invasion in two landscapes that differed in composition and structure. One of the surveyed landscape was more dominated by urban habitats and exhibited higher fragmentation of habitats in contrast to the more agricultural/forested landscape exhibiting lower level of fragmentation. Despite those differences, patterns of invasion were very similar between the two studied landscapes.

Global invasion levels were very similar in the two landscapes, not only because the total density of invasive populations was very similar, but also because density of individual species were in the same order of magnitude. Based on predictions derived from the theories of invasion biology, one may have hypothesised a higher invasive success in the Ke landscape for two reasons. First, as it has been shown that exotic plants commonly dominate disturbed habitats (Aguiar *et al.*, 2001; Brothers and Spingarn, 1992; Cohen, 2002; Hobbs and Huenneke, 1992; Parker and Reichard, 1998), one would have expected a higher level of invasion in the more urban landscape. Second, more fragmented landscapes harbour higher edges density that are supposed to be structural elements more susceptible to invasion (Harrison *et al.*, 2001; With, 2002).

In addition, habitat selected by invasive species were very similar in the two landscapes studied but also among the different species. Anthropic habitats with a high probability of perturbation occurrences (ruderals, urban industrial, urban non industrial) were selected by all species in at least one landscape. In addition, more natural habitats including natural/semi-natural grasslands and broadleaved forest were selected indicating that the invasion extend well beyond the first stages of introduction. An interesting point was the lack of relationships between the density of species populations at the landscape scale and their ability to invade natural/semi-natural habitats indicating that impacts of invasion may be important at its very first stage.

We found a strong relationships among landscape structure and the pattern of population distribution only for patch area. For all the cases examined, except one, larger patch of selected habitat were more prone to host the target species. Patch size may be linked to probabilities of local population persistence through stochastic process affecting small populations, but also to colonization probability due to differential probabilities of diaspore reaching patches of different sizes. The positive effect of patch connectivity on the probability of Impatiens glandilufera populations occurrence is consistent with a 'propagule pressure' hypothesis. A patch of habitat surrounded by a higher proportion of selected habitat, and potentially by a higher density of invasive populations, is more likely to receive a higher propagule input that would promote colonization. Nevertheless, this hypothesis this relationship was consistent across landscapes only for *I. Glandulifera*. This is noteworthy that it concerned only the species colonizing primarily linear habitats (river banks).The low influence of patch isolation on invasion patterns suggests that dispersal capacities of the studied species largely overcome the scale of the study or that other factors should be taken into account to explain invasive populations distribution. Human activities, generating disturbed habitats, are one of the most important vector of dispersion of the invasive species but is very difficult to assess when working at the landscape scale. We demonstrated that micro habitats play an important role in providing suitable habitats for invasive species. Then, the availability of micro-habitats within selected habitat patches may be a more important factor influencing the distribution of invasive species at the landscape scale than the spatial structure of the habitats. Roads and streams are generally considered to serve multiple functions that enhance exotic species invasions. They may act as corridors for dispersal, provide suitable habitat for establishment and contain reservoirs of propagules for future episodes of invasion (Parendes & Jones, 2000; Watkins *et al.*, 2003). Our results are in agreement with previous evidence that roadsides and river banks are the first landscape elements to be colonized by alien species (Pauchard & Alaback, 2004). Our results stressed that linear networks, such as rivers banks and roads, play an important role in the distribution of invasive plant species at the landscape scale.

To our knowledge this is one of the first quantitative analysis of population dynamics at the landscape level for invasive species. The species exhibited quite different relative increase rates between the two years of survey, which is apparently independent of the initial density of populations. For some species, the landscape is far from being saturated and invasion is still in its exponential stage urging for immediate actions to control species extension. For species with a low initial density of populations, such as *H. mantegazianum*, the species may still be eradicated from the landscape. For species with a higher initial density of populations and high increase rate, monitoring of selected habitats and eradication of new nascent foci will help controlling the invasion at the landscape scale. In contrast, for species with high density and current low increase rates, priority should be given to control and mitigation of impacts of established populations.

3.4 Link between invasive success, seed dispersal ecology and habitat selection.

Previous studies have hypothesized that invasive species owed their success to their ability to thrive in a wide variety of habitats or environment. Such studies have found that the degree of habitat generalization is a good indicator of invasion success (Marvier *et al.*, 2004). Consequently, *I. glandulifera* and *Fallopia* spp. may be considered as the most successful invaders in the studied landscapes because they selected more habitat types than other species. Whether this success of invasion is linked to better dispersal ability is also a matter of interest. From our results, it is difficult to assess precisely the relationship between invasive success based on population density/habitat selection and dispersal traits because of the limited number of species considered (which is inherent to detailed studies). Nevertheless, some trends owe to be considered. An important seed production did not always explain a high invasive success. *I. glandulifera* produces less seeds (2500/plant *from* Koenies & Glavac, 1979; .seed rain = 6000, *from* Beerling & Perrins, 1993) than *S. inaequidens* but is more successful in the studied landscape. No persistent seed bank does not seem to be a disadvantage: *I. glandulifera* and *Fallopia* spp. do not develop persistent seed bank, but are very successful in the studied landscapes. Considering germination level, the more successful invasive species do not germinate very well (*I. glandulifera*: 0,4 ± 1,2-2 ± 2 % for fresh seeds, 16,4 ± 11,9 – 72,9 ± 17,5 % for stratified seeds *from* Fortemps, 2004). The ecology of seeds did not seem to be a good predictor of invasion success for the studied cases.

B C4 GRASSES IN AND ALONG MAIZE FIELDS: DISTRIBUTION, DISPERSAL AND POPULATION DYNAMICS.

1. Material and Methods

Level 1 – In 2004 and 2005 320 IFBL grid units (each 1 km^2) were inventoried. During prospection our main concern was to document the presence of C_4 grasses in maize fields, but occurrences in other habitats were also separately recorded. An effort was made to apply the same prospection intensity in each square, but with time investment somewhat higher in squares with more maize cultivation. The results could be compared with a previous survey in 1999-2000 (Hoste & Verloove 2001).

Level 2 – For the more detailed mapping and monitoring of populations in a restricted area we selected *Setaria faberi* and *Digitaria aequiglumis*. In Belgium both species are believed to be recent arrivals in the agricultural landscape, although herbarium specimens of ephemeral casuals of the first species have been collected since at least 1977. For each species a different area was selected and intensively surveyed in 2003, located in Zomergem-Hansbeke-Merendree and Sleidinge respectively. Each population and the trajectory followed during prospection were indicated on a map. The trajectory was primarily dictated by the location of maize fields within our selected area. In both 2004 and 2005 the survey was repeated, following the same trajectory.

Level 3 – In 2003 29 transects, each 25 m long, were selected along maize fields; 2 extra transects were selected along a road verge. The transects were selected on the basis of several criteria, such as the presence well developed vegetations with a mix of C_4 grass species and with abundance varying along the 25 m transect. A number of transects were chosen because both *Echinochloa crus-galli* and *E. muricata* were present. Each transect was divided in 25 units (each 1 m long). The presence and abundance of C_4 grasses in each unit was described, taking into account the different microhabitats (border of the adjoining road verge, the strip of ploughed land just outside the external row of maize plants, and the strip between the first and second rows of plants). In dense populations counting the number of plants, which furthermore vary between small and large, is very difficult; we therefore chose the number of flowering stems as an indicator of abundance. A short description of the habitat and a species list of vascular plants were added for each transect.

2. Results

2.1 Level 1 – Prospection of a 320 km^2 area

The results of our prospection of a 320 km^2 area are presented in Table 10. In 2004-2005 most species were found in an increased number of 1 km^2 units as compared with 1999-2000.

***Table 10** – Distribution of C_4 grasses in a 320 km^2 area between Bruges and Ghent. The last column shows the number of units where a species was only found in habitats not connected with maize cultivation.*

	1999-2000		**2004-2005**		
	1 km^2 units	**%**	**1 km^2 units**	**%**	**not associated with maize**
Digitaria aequiglumis	0	0	1	<1	0
D. ischaemum	133	42	262	82	0
D. sanguinalis	83	26	155	48	26
Echinochloa crus-galli	315	98	320	100	5
E. muricata	?	?	254	79	7
Panicum capillare	2	1	3	1	0
P. dichotomiflorum	104	33	188	59	3
P. miliaceum	15	5	13	4	6
P. schinzii	0	0	3	1	0
Setaria faberi	23	7	66	21	5
S. italica	7	2	3	1	2
S. pumila	19	6	36	11	12
S. verticillata	271	85	288	90	0
S. v. var. *ambigua*	55	17	77	24	2
S. viridis	77	24	93	29	17

The interpretation of these changes is not straightforward. It should be taken into account that in 1999-2000 prospection was carried out less intensively. A more intensive prospection produces different levels of increase for different species: rather discrete species (e.g. *Digitaria ischaemum* and *D. sanguinalis*) score relatively better; also, in the case of a pair of similar looking species, the rarer one might score better when prospection is intensified (e.g. *Setaria verticillata* var. *ambigua* and *S. v.* var. *verticillata*). On the other hand, the increase of numbers for *Panicum dichotomiflorum* and *Setaria faberi* seems to reflect more than only an intensified prospection effort. For both species the distribution in 1999-2000 and 2004-2005 shows the same phenomenon of an expanding core area, surrounded by a number of more isolated populations (Figure 24).

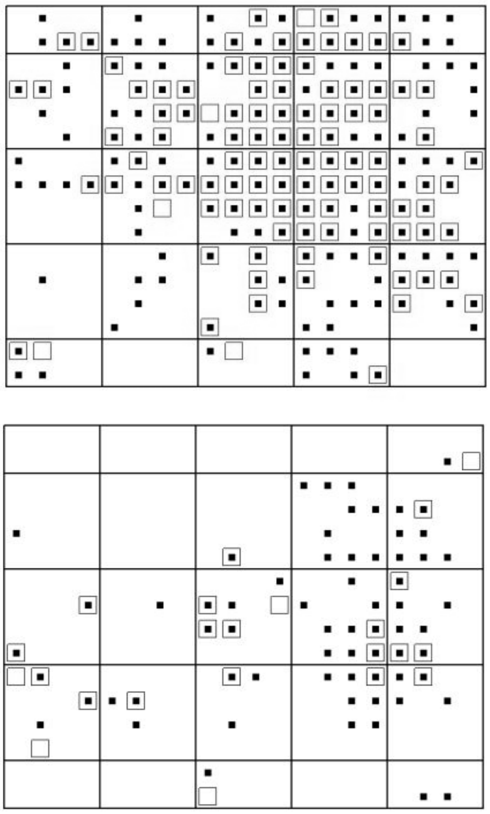


***Figure. 24** – The distribution of **Panicum dichotomiflorum** (top) and **Setaria faberi** (bottom) in a 320 km^2 area between Bruges and Ghent: open squares 1999-2000; small dots 2004-2005.*

In 2004-2005 prospection was somewhat more focused on maize fields than in 1999-2000. This probably explains why species which are less dependant on maize fields, such as the bird-seed aliens *Panicum miliaceum* en *Setaria italica*, show no increase (but numbers are altogether low). The strong increase of *D. sanguinalis*, a species often found outside maize fields, such as the bird-seed aliens *Panicum miliaceum* en *Setaria italica*, show no increase (but numbers are altogether low). The strong increase of *D. sanguinalis*, a species often found outside maize fields, could indicate a real increase resulting from an ongoing habitat extension into the very much expanded habitat of maize fields.

In 1999-2000 *Echinochloa muricata* had only recently been added to the Belgian flora and was only known from a restricted number of locations in Limburg. Between Bruges and Ghent it went unnoticed until 2001, but in 2004-2005 it was found in 79 % of our grid units. Its abundance and the presence of several clearly distinct forms – recognizable in the field but of unknown taxonomical value – suggest a long overlooked presence with multiple introductions and a rapid extension into maize fields; see also Hoste (2004).

2.2 Level 2 – Mapping the distribution of populations of Digitaria aequiglumis and Setaria faberi

While monitoring populations of two species in two different areas during a three- years period terms such as ‘populations’ or ‘locations’ had to be defined in a rather pragmatic way. At most locations maize cultivation went on without interruption for three years. In these parcels the pattern of distribution (that is: the exact location of populations) hardly changed at all, but the number of plants could sometimes fluctuate strongly. Three years proved to be to short a period to assess larger geographical trends of dispersal. The number of ‘locations’ where *Setaria faberi* was found had clearly grown after three years, but this might in large part be due to the growing amount of information built up over a period of three years of field work. Finding a ‘new’ and rather striking population in the third year of field work raised questions such as “Have I overlooked this in previous years?” or “Is this a new population, resulting from an introduction of seeds by an agricultural contractor?” or “Was this population perhaps only present in the form of a seed bank in the past one or two years?”.

In a few cases we clearly documented the complete ‘disappearance’ of *Digitaria aequiglumis* when maize was replaced with another crop (cereals) in the second year of our field work, only to pop up again (at the same location within the parcel) in the third year, when maize cultivation was resumed.

Level 3 – Monitoring of transects along maize fields

Similar patterns of stability of precise location within a parcel combined with strong population fluctuations were also revealed by our 25 m transects along maize fields. The distribution of each different species along a transect most often showed considerable stability. This strongly indicates that a new input of seeds from the outside is not needed to keep populations healthy and therefore in the agricultural landscape most C_4 grasses should be accepted as naturalized (or at least naturalizing) species. An exception to the rule are bird-seed aliens that sometimes thrive as casuals in the border of maize fields.

3. Discussion

Although the project allowed for only three years of monitoring and although important information is lacking (e.g. details on the nature and timing of herbicide use and other agricultural activities on parcels with populations of C_4 grasses), some general conclusions can be formulated. The history of the expansion of C_4 grasses in Belgium is very closely associated with the upsurge of maize cultivation during the past three decades. Whenever cultivation of this crop on a parcel is interrupted C_4 grasses tend to ‘disappear’ (almost) completely. Through the production of numerous seeds and a viable seed bank that easily spans several years (Dekker 2003), the species may pop up again when maize cultivation is resumed. But even without such interruptions, minor shifts in the timing of ploughing, sowing, and herbicide use, often linked with exceptional weather, can result in a dramatic reduction or increase of populations from year to year. Such dynamic processes tend to obscure another reality: C_4 grasses have a poor dispersal capacity and are highly dependent on human activities, such as agricultural contractors, to travel from one parcel to another. Once introduced into an agricultural landscape C_4 grasses are capable of building up populations that are no longer dependant on the renewed entry of seeds from the outside. Given a continuation of today’s maize cultivation practices, it is to be expected that species with a currently limited distribution will continue to gain new ground in several different parts of Flanders. So far there are no indications that they threaten to invade habitats with a high conservation value.

SECTION 4: CATALOGUE OF NEOPHYTES IN BELGIUM (1800-2005) AND INVASION HISTORIES

A CATALOGUE OF NEOPHYTES IN BELGIUM (1800-2005)

1. Material and methods

The present catalogue is entirely based on a thorough and critical revision of the main Belgian public herbaria and some smaller but relevant private herbaria. Some critical groups have been revised by world experts for particular genera or by experts for alien plants in general. All revised collections (over 25.000) have been databased which enabled us to compile a catalogue that provides the following information for each taxon:

- Name of the taxon;
- Synonym;
- Family to which the taxon belongs;
- Mode of introduction (deliberate / accidental);
- First known record;
- Most recent record;
- Geographic origin;
- Presence in the 3 political units of Belgium (Flanders – Brussels – Wallonia);
- Degree of naturalization (in order to assess invasion success for each taxon: casual – naturalized – invasive);
- Vector of introduction (horticulture, grain, wool, ores, …).

Only neophytes (i.c. post 1500 - introductions) have been taken into account. Archaeophytes are excluded from the list. Assessing native / non-native and neophyte / archaeophyte status sometimes proved to be critical. The criteria for inclusion or exclusion in the catalogue are discussed in detail.

2. Results

2.1 General results

At present 1917 taxa are included in the catalogue. Of these 366 (19%) have not been reported before from Belgium: they have been recorded for the first time in very recent times, or they have been collected in the past but remained unidentified / erroneously identified up to now, or they have been reported before but were considered to be doubtful up to present. On the other hand at least 29 taxa need to be omitted from the Belgian flora list (formerly included in error).

Statistics

- 139 families are represented but only 8 count for more than 50 taxa each: they represent 1035 taxa (54%); the largest families are Poaceae (n = 316; 16,4%) and Asteraceae (n = 238; 12,4%):

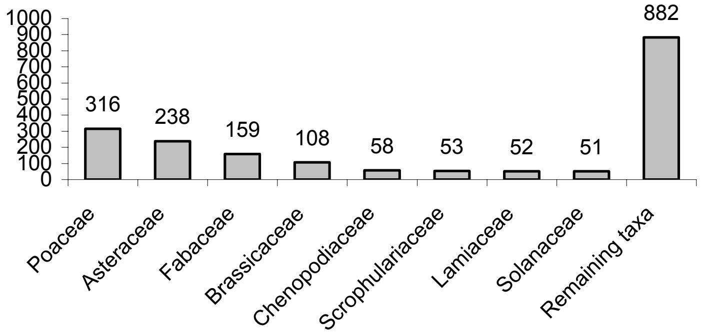


Figure 25 *– Taxonomic diversity of the Belgian non-native flora*

- At least 829 taxa (43,2%) have been introduced (exclusively or primarily) deliberately, usually as horticultural plants:

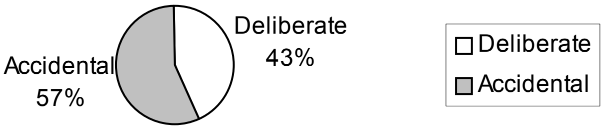


Figure 26 *– Mode of introduction of the Belgian non-native flora*

- The majority of the taxa is of Eurasian origin (55,2%), the number of New World taxa is relatively restricted (17,6%):

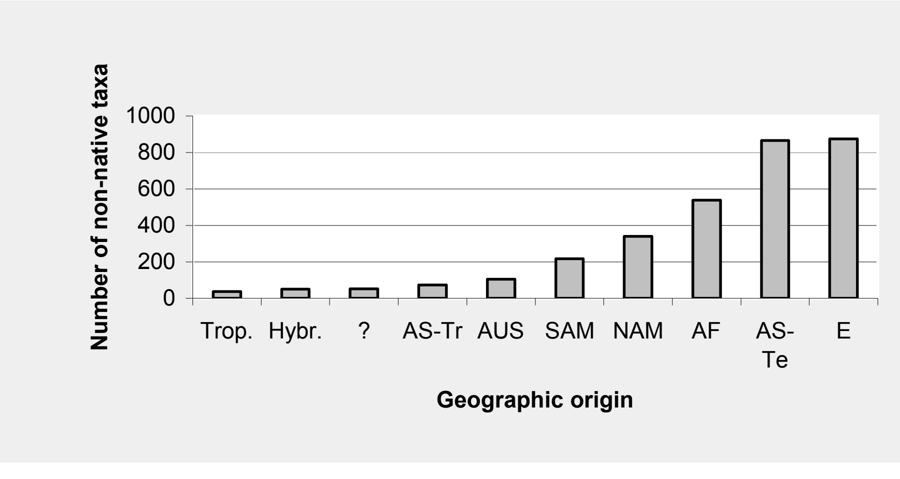


Figure 27 *– Geographic diversity of the Belgian non-native flora*

- 352 taxa (18,3%) are considered to be fully naturalized [1], a large majority (n = 1483; 77,3%) is strictly ephemeral; the remaining taxa (less than 5%) are of +/- uncertain status:

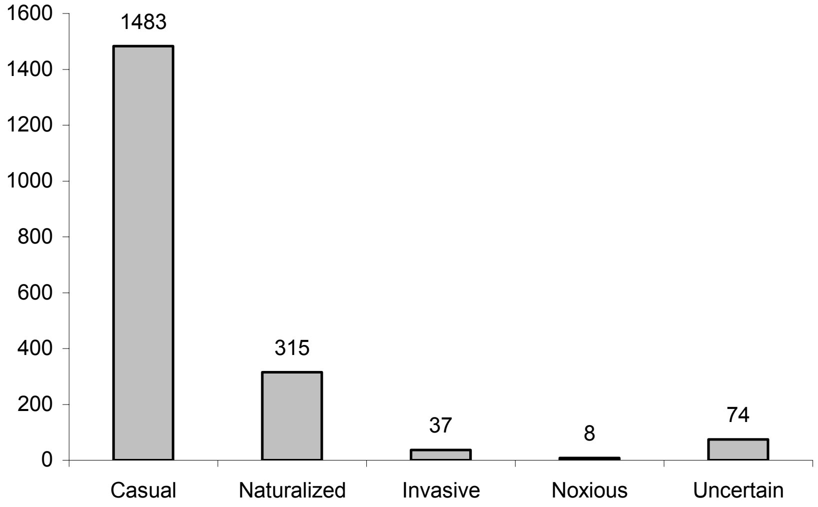


Figure 28 *– The invasion success (degree of naturalization) of the Belgian non-native flora*

- The number of introductions seems to increase: nearly 16% (n = 306) has been recorded for the first time posterior to 1990:

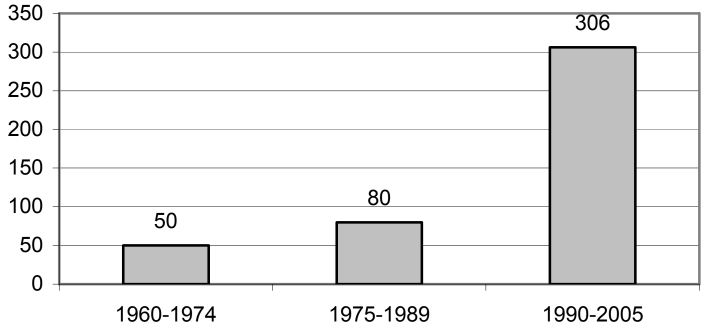


Figure 29 *– The number of new plant introductions in the past 45 years in Belgium*

2.2 Specific results concerning naturalized / invasive taxa

- The catalogue was intended as a list of all not-indigenous vascular plants that occur or have occurred in Belgium, but not as the final oracle on the grouping of those plants into invasive or not invasive species. Existing popular definitions to separate both these categories do not resist a critical analysis. The matter should be subjected to a fundamental discussion between all

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[1] Definitions: casual = soon disappearing after its initial introduction, not or scarcely able to reproduce; naturalized = reproducing sexually or non-sexually and hence able to build up self-sustainable populations independent from the initial introduction; invasive = naturalized taxa penetrating and proliferating in (semi-) natural habitats; noxious = invasive taxa causing damage in one or various areas (biodiversity, economy, health).

people concerned, at least at the national level. So the following percentages have to be considered as provisional.

- The number of invasive taxa (sometimes exceedingly difficult to assess whether invasive or not) appears to be restricted. At present perhaps not more than 37 taxa (less than 2% of the total number or 10,5% of the number of naturalized taxa) proliferate in more or less natural or semi-natural habitats; several more are sometimes found in similar habitats but their presence is modest or temporarily.
- The number of taxa actually causing damage in areas of biodiversity, health and/or economy is probably limited to 8 (less than 0,5%): *Fallopia japonica*, *Heracleum mantegazzianum*, *Hydrocotyle ranunculoides*, *Impatiens glandulifera*, *Ludwigia grandiflora*, *Prunus serotina*, *Rhododendron ponticum* and *Rosa rugosa*.
- At least 215 taxa (61%) of the naturalized / invasive taxa have been introduced deliberately (markedly more than for the complete catalogue); moreover, all of the taxa causing damage are deliberate introductions.

3. Discussion

With its highly developed motor-, rail- and waterway network and as an important international trade center Belgium is prone to plant introductions. Despite its small surface a remarkably high number of non-native plant species has been recorded in relatively recent times and this number seems to increase rapidly.

A large majority of these introductions remains strictly ephemeral and is not really a part of the Belgian flora. On the other hand almost 20% of the introductions are able to survive and become naturalized. Moreover, the number of naturalizations seems to increase in recent times. At present the number of invasive and noxious taxa is restricted but this might change soon.

A surprisingly high number of the introductions are deliberate entries; they have been introduced chiefly through horticulture. The number of deliberate introductions is still higher within the naturalized and invasive taxa and all (!) taxa presently causing damage in one way or another are deliberate introductions and thus could have been prevented. This surely constitutes as import message towards policy- and decision makers.

B INVASION HISTORIES

1. Material and methods

The available floristic data in Belgium consist of the information given by literature (±1800-now), the labels on herbarium sheets (±1850-now), the first IFBL-mapping (1939-1971) (IFBL: Instituut voor de Floristiek van België en Luxemburg / Institut Floristique Belgo-Luxembourgeoise.), the second IFBL-mapping (1972-1992), the Flo.Wer-mapping of Flanders and Brussels (1992-2004) (Flo.Wer: Floristische Werkgroepen, a public association) and the AEF-mapping of Brussels and Wallonia (1992-) (A.E.F.: Amicale Européenne de Floristique, a public association). Herbarium and literature data are at everybody’s disposal and can easily be brought together. For the specific floristic mapping-data the situation is more complicated since they are under different management rules and in some cases they had to be digitalized first. Table 1 gives the number of observations (each time a unique combination of species, observer, place and time) that could be drawn from the herbarium sheet. The situation was far more complicated for the other data-sources. The IFBl-1 data had been digitalized before only at the synthetic scale of 16 km²-squares (“uurhokken”) and without any reference to dates and observers and hence were not suited for our goals. However, the original field lists for this cartography being kept at the National Botanical Garden they could be re-digitalized during the INPLANBEL-project for the whole of the national territory. The same is true for the field lists of the IFBL-2 period (1972-1992) and those too have been digitalized for the selected species and the corresponding circumstantial data, but only for the Walloon region since the work for Flanders had been done before (VLINA-project 1996-1999) and these data were put at our disposal by Flo.Wer. The digitalization of the IFBL lists took 24 months and was finished only at the end of the 3-years INPLANBEL-project. The acquisition of the recent (post 1992) floristic data concerning the Walloon region still remains problematic, especially for the circumstantial information. The species-specific data will be acquired soon, but it is still unclear to what extent these will be complete.

***Table 11** – Numbers of specimens in the major Belgian herbaria of the neophyte taxa selected for the analysis of their dispersal history in Belgium*

	BR	LG	GENT	Σ
Amaranthus retroflexus	**191**	**32**	**46**	**269**
Barbarea stricta	*19*	*1*	*7*	*27*
Cerastium tomentosum	-	-	-	-
Chenopodium ambrosioides	68	26	14	108
Coronopus didymus	120	23	36	179
Cyperus esculentus	6	1	6	13
Digitaria sanguinalis	212	36	29	277
Echinochloa crus-galli	205	78	34	317
Elodea Canadensis	158	46	20	224
Elodea nuttallii	58	16	13	87
Epilobium ciliatum	85	28	12	125
Eragrostis minor	121	29	16	166
Fallopia japonica	60	21	8	89
Fallopia sachalinensis (incl. *F.* x *bohemica*)	21 (32)	5	8 (15)	34 (52)
Galinsoga parviflora	95	11	6	112
Galinsoga quadriradiata	94	22	8	124
Geranium pyrenaicum	214	57	23	294
Heracleum mantegazzianum	45	1	0	46
Impatiens glandulifera	59	16	7	82
Impatiens parviflora	102	30	10	142
Juncus tenuis	287	55	37	379
Lathyrus latifolius	47	26	8	81
Lepidium virginicum	184	24	29	237
Oxalis corniculata	114	19	15	148
Polemonium caeruleum	***39***	***11***	***1***	***51***
Prunus serotina	***82***	***19***	***2***	***103***
Rosa rugosa	***21***	***6***	***4***	***31***
Senecio inaequidens	***122***	***40***	***10***	***172***
Setaria verticillata	157	38	36	231
Solidago canadensis	34	13	2	49
Solidago giganteum	72	17	11	100
Veronica peregrina	129	21	21	171
Xanthium orientale	27	5	0	32
Σ	3259	773	486	4518

BR: National Botanic Garden, LG: Botanical Institute of the Liège University, GENT: Botanical Institute of the Ghent University. Taxa in bold where studied for different aspects by other project partners.

At the National Botanic Garden all data were stocked in Excel and Access-files. External data were delivered in different formats. The final database will be shaped in the Access-format.

Period- and source-specific subsets of data (<1939, 1939-1971 and 1972-present) are calibrated and framed in two successive steps. (1) The species-specific data from within a certain period are compared with the global data (including all collected alien species) in that same period. This makes it possible to eliminate those parts of the territory for which no relevant information can be expected. (2) The knowledge on the personal floristic activities and behaviour of the collectors that were familiar with the specific alien species in the different periods – Who knew those species? When and where did they find those species? Where and when did they not? – will sharpen the picture of real invasion histories. Note that these methods cannot replace lacking information. They can only help in reducing errors in the interpretation of the changing distribution patterns.

2. Results

Given the complex situation of the regionalized and decentralized management of floristic data in Belgium, the construction of one global dataset on selected alien plants will represent a result on its own. Within the period of the INPLANBEL-project we only succeeded partially. Most information about Wallonia for the period after 1992 is still lacking in the database. There is good hope, however, that at least the direct information on the species' distribution will be available soon, but it still remains uncertain whether or not we will be able to use the corresponding circumstantial information.

The analysis of a partial dataset (Flanders with the Brussels Capital Region) was an alternative possibility, but then only after the finishing of the digitalization of the IFBL-1 data and with the unpleasant prospect of being obliged to restart the analyses somewhere halfway. To some degree this is what has been executed in commenting the distribution maps in the "Atlas van Vlaanderen en het Brussels Gewest" (Van Landuyt *et al.* 2006), however without the calibration for circumstantial conditions and with only an intuitive period framing of the data. Deadlines have been passed since long now and if the Walloon data are not acquired by the end of May 2006 the analyses will be executed in an asymmetrical way (on the Belgian scale for the period until 1992) or for Flanders and Brussels for all periods.

The necessity of source-specific (and hence period-specific) framing is illustrated by Figure 30 that shows that for the selected 32 neophytes the number of observations based on herbarium collection gives no indication at all on the frequency of these species[2]. In fact, the reasons why herbarium specimens have or have not been collected are diverse.

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[2] Since recent frequency-figures (number of grid-units) are not available at the scale of Belgium, the frequency-figures at the scale of Flanders and the Brussels Capital Region have been used (figures after Van Landuyt *et al.* 2006)

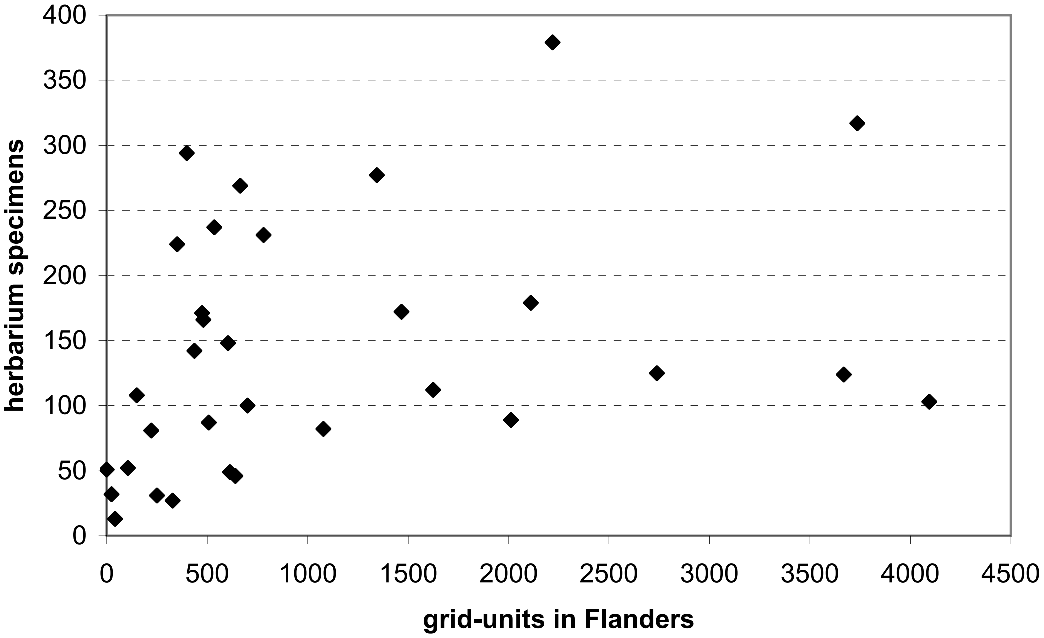

Figure 30 *.– Comparison between the number of herbarium-sheets and the number of grid-units for 32 selected invasive species in Belgium ($r^2 = 0.1007$, without Echinochloa crus-galli and Juncus tenuis even less: $r^2 = 0.0127$): the two variables are independent.*

So, the interpretation of expanding distributions (shown by the ‘raw material’ of successive distribution maps in a chronological sequence) as invasive behavior becomes really hazardous if the data for one of the compared periods relies exclusively on incidental information such as herbarium collections and literature citations, which is the case for the whole of the pre-IFBL period (<1939).

The differences between both periods of systematic mapping (1939-1971 and 1972-2004) might be smaller, but still are considerable as is illustrated by Figure 31 that shows for Flanders and the Brussels Capital Region the obvious spatial differences between both mapping periods and, more in general, the differences in fieldwork efforts.

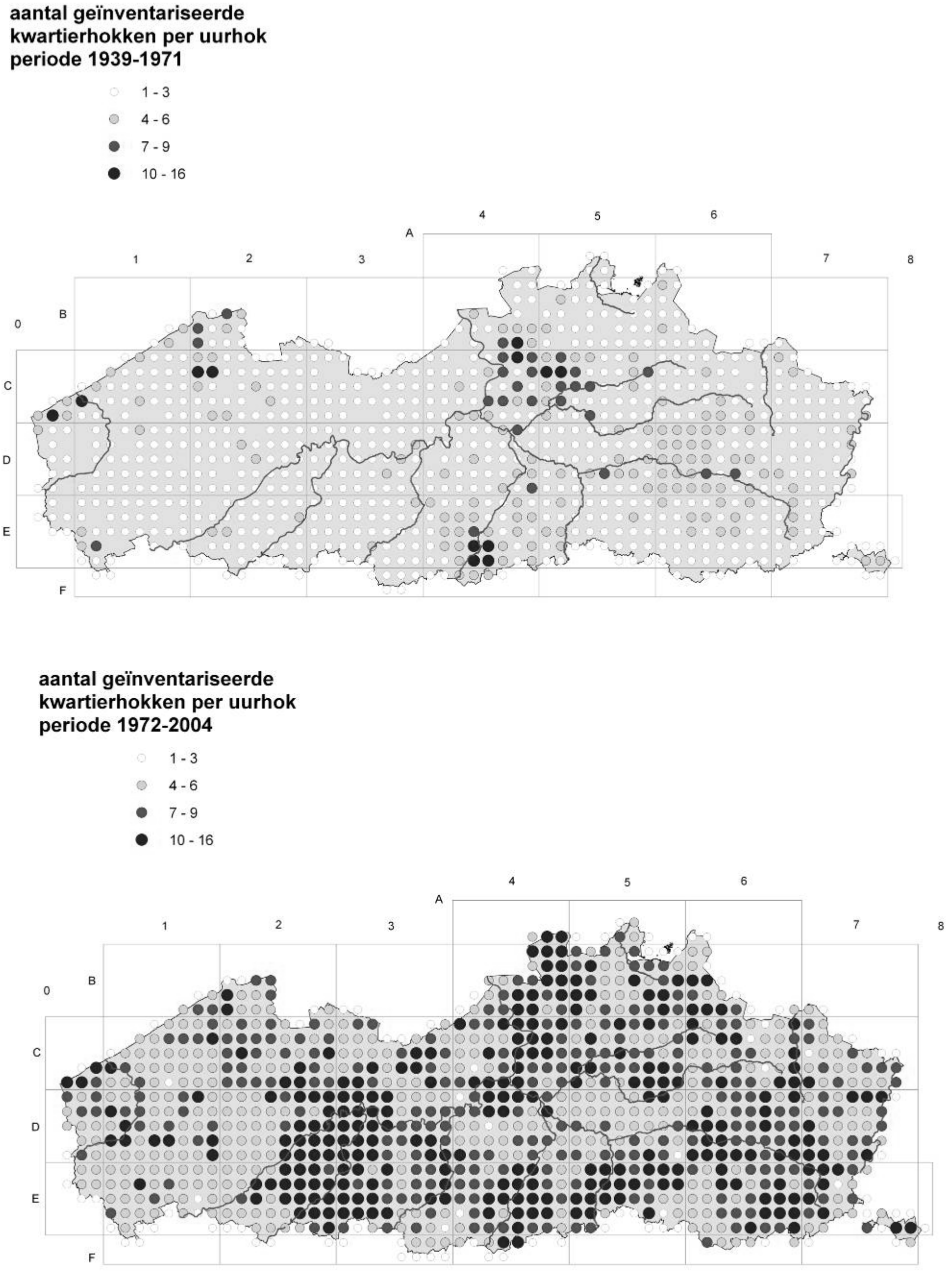

***Figure 31**- Number of 1x1 km squares that have been surveyed in each 16 km² squares in the periods 1939-1971 and 1972-2004 in Flanders*
(source: Van Landuyt W, Vanhecke L & Hoste I, 2006)

3. Discussion

Obviously, even the comparison of the distribution data from both systematic mapping periods needs calibration and period-specific framing. Therefore any analysis without those correcting factors remains tentative. However it is interesting already to develop a system to qualify the different development types of the selected neophytes based on the evolution of their distribution patterns and frequencies between both mapping periods [3]. It is possible to distinguish different spatial development phases between the first arrival of a new invading species and its maximal distribution after its invasion has been completed. Within a theoretical concept these empirical expansion stage can be identified with sections on mathematical growth curves.

1. Absence of the species.
2. Presence in few, isolated grid-units.
3. Presence in several isolated grid-units, and/or locally present in several concatenate grid-units.
4. Sub-regional or zonal (e.g. waterways) presence.
5. (Almost) covering "natural" (sub)-regions for the larger part.
6. (Almost) covering the complete map area.

When comparing the (un-calibrated!) distribution data of both systematic mapping periods for Flanders the following development types can distinguished for the 32 selected neophytes [4]:

Table 12 *– Types of distribution dynamics*

Type	Phases evolution	Examples
1	2 > 5	*Senecio inaequidens, Solidago canadensis* [5]*, S. gigantea*
2	4 > 6	*Epilobium ciliatum*, *Fallopia japonica*
3	3 > 5	*Digitaria sanguinalis, Impatiens glandulifera*
4	2 > 4	*Barbarea stricta, Heracleum mantegazzianum, Setaria verticillata, Veronica peregrina*
5	1 > 3	*Cyperus esculentus, Xanthium orientale*
6	5 > 6	*Echinochloa crus-galli, Galinsoga quadriradiata*
7	4 > 5	*Coronopus didymus*
8	3 > 4	*Amaranthus retroflexus, Elodea nuttallii, Lepidium virginicum, Oxalis corniculata*
9	2 > 3	*Chenopodium ambrosioides, Eragrostis minor, Fallopia sachalinensis, Impatiens parviflorum, Lathyrus latifolius, Rosa rugosa.*
10	5 > 5	*Prunus serotina, Galinsoga parviflorum, Juncus tenuis*
11	4 > 4	*Elodea canadensis, Geranium pyrenaicum*

In Type 1 the changes in distribution and frequency cover three development phases, in Types 2-5 two development phases are bridged, in Types 6-9 one development phase is bridged and in Types 10 and 11 the situation is almost stagnant or even reclining. Obviously these development types can function as a measure for invasive success.

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[3] The differences between both these periods and the period of incidental data (<1939) is much to profound to be executed without any calibrating.

[4] *Polemonium caeruleum* is not naturalized in Flanders and was omitted.

[5] Both *Solidago* species should probably be degraded to a "lower" class.

GENERAL DISCUSSION

1. The main lessons from the different tasks :

1.1 Is it possible to predict invasion on the basis of a species x sites analysis?

Since the invasion of large exotic plant species often has severe consequences for neighbouring native plants (through competition for resources), and since successfully reproducing invaders represent a risk for neighbouring ecosystems (through high propagule pressure), determining which traits maximize components of invasive success is an important element of predicting invasions. At each site we characterized traits of the invasive species, traits of the invasible ecosystem, and individual growth and fitness of the invaders as a component of their invasive success. Growth or fitness were regressed on all possible combinations of one plant and one ecosystem trait at the time, assuming that specific matches between traits could be at the basis of successful invasions. The data confirm our starting hypothesis: invader success, expressed as invader growth or seed production, can be explained by combining traits of the invader with traits of the invaded ecosystem. For growth, the most promising models comprised plant traits such as specific leaf area or nutrient resorption, and ecosystem traits such as community biomass, its nutrient concentration, or light transmission. For fitness, combining invader growth (height, biomass) or nutrients in senescent leaves, with a soil carbon related trait or nutrient concentration of the community, looks promising. The combined approach explained up to 80% of the variance, which was significantly more than one-sided invasiveness and invasibility approaches that use only invader or invaded ecosystem traits. The best traits should get priority in validation studies.

1.2 Do invasive plant species modify ecosystems properties ?

The direct impacts of exotics species invasions on the structure of ecosystems are often readily apparent and clearly appreciated. However, the potential for more subtle alterations of ecosystem processes has received little attention, particularly in Europe. As plant traits and ecosystem processes are closely connected, the substitution of dominant exotics for native species may result in alterations of biogeochemical cycles and soil chemistry through differences in resource acquisition and utilisation and/or through indirect effects on soil biota. First, increased aboveground productivity was noted in nearly all invaded ecosystems whatever the invasive species. This increased productivity is doubtless one of the characters that may explain the success of invasion and also the reduction of species richness in invaded zones (through competition for light). The consequences of increased productivity on carbon pools and fluxes need to be investigated at the landscape scale. Concerning nutrients in plants, mostly due to high biomass and for certain species also to higher nutrient concentration (example: K for both *Impatiens* species), invasive alien species had higher nutrient stocks in aboveground biomass compared to indigenous uninvaded vegetation. Higher nutrient stocks most likely resulted in increased nutrient return in litterfall which in turn may accelerate nutrient cycling in invaded zones. Concerning soil properties, there was a tendency for invasive alien species to increase nutrient availability in invaded zones.

Future work should focus on the mechanisms of impacts on soil. In particular, the hypothesis of nutrient uplift in *F. japonica* definitely deserves further investigation. Also, impacts on organic matter dynamics in topsoil have not been considered here. Detailed analyses of dynamics of organic matter decomposition are necessary to clarify the mechanism underlying the somewhat complex pattern found for nitrogen. Secondly, the question arises as to the consequences of soil impacts on biodiversity. Altered soil composition can conceivably modify competitive relations between invasive alien species and native vegetation. Increased competitive ability of invasive alien species on their own soil would provide evidence for positive feed-back effects. Thirdly, altered soil composition may have far-reaching consequences on other trophic levels, including soil microbial communities and soil fauna. Finally, the consequences of soil impacts on restoration also need investigation. The possibility of carry over effects (i.e. long–lasting soil alterations after removal of invasive alien species) must be examined.

1.3 What are the driving factors of invasion at the landscape scale ?

We described the spatial pattern of populations in two different landscape units by surveying and localizing all populations of target species. Based on population number, *I. glandulifera* exhibited the highest invasive success in both landscapes. Habitat selection indices indicated that some habitats were more prone to invasion than expected under a random distribution hypothesis. Habitat selection differed according to species. Based on the number of selected habitats, *F. japonica* in the first landscape and *I. glandulifera* in the second landscape exhibited the highest invasive success. The influence of roads, rivers and railways networks on the distribution of populations was also examined. Roads, rivers and railways networks represented respectively 9% and 15% of the landscape unit area. Landscape networks played an important role as dispersal corridors. The influence of patch spatial characteristics (surface, shape, isolation) on presence/absence of species was assessed by logistic regressions. Patch area was the most important characteristic influencing probability of invasive species occurrence.

Concerning the dynamics maize field tropical C4 grasses in the agricultural landscapes, the history of expansion is closely associated with the upsurge of maize cultivation during the three past decades. These species have a poor dispersal capacity and are highly dependent on human activities to travel from one parcel to another. For both studied species, the distribution in 1999-2000 and 2004-2005 shows the same phenomenon of an expanding core area, surrounded by a number of more isolated populations. The strong increase of D. sanguinalis, a species often found outside maize fields, could indicate a real increase resulting from an ongoing habitat extension into the very much expanded habitat of maize fields. a new input of seeds from the outside is not needed to keep populations healthy and therefore in the agricultural landscape most C4 grasses should be accepted as naturalized (or at least naturalizing) species. An exception to the rule are bird-seed aliens that sometimes thrive as casuals in the border of maize fields. C4 grasses will certainly extend their range as a result of current maize cultivation practices.

1.4 Alien flora in Belgium.

In Belgium, 139 families of alien species are represented but only 8 count for more than 50 taxa each. The largest families are Poaceae and Asteraceae. At least 829 taxa (43,2%) have been introduced (exclusively or primarily) deliberately, usually as horticultural plants. The majority of the taxa is of Eurasian origin and the number of New World taxa is relatively restricted. About 20% of taxa are considered to be fully naturalized, a large majority (77,3%) is strictly ephemeral. At present, about 37 taxa (less than 2% of the total number or 10,5% of the number of naturalized taxa) proliferate in more or less natural or semi-natural habitats; several more are sometimes found in similar habitats but their presence is modest or temporarily.

The completion of the catalogue of neophytes in Belgium provides a good base for a sound assessment of their naturalization status and their behaviour in relation to invasion processes. However, the final judgment in these matters should be subjected to a broad discussion among experienced botanists to sharpen the possible criteria. Existing recent systems for the classification of naturalizing and invasive plants (such as Richardson *et al.* 2000 and Pyšek P *et al.* 2004), have the merit of simplifying complicated earlier systems, but do not withstand a critical analysis because some of the criteria they use are questionable. Many problems with the status attribution could be avoided by simply replacing the term “invasive species” by “invading species”. By untying the invasive potential of species from the invasion processes, and by accepting that being invasive is a temporal, transient state in which every innocent species can get, in particular circumstances, it is more easy to focus on the real invasion processes and the active invaders at any scale.

During the INPLANBEL-project the gathering of information on the distribution of the selected species at the Belgian scale proved to be very difficult and it became a major obstruction in the progress of this analysis. It therefore follows that in the future the construction of one operational floristic database at the national Belgian scale is highly recommended.

2. From a management point of view

From the ‘species x sites’ analysis, a classification can be made on a mechanistic basis (1) of species according to the risk they represent, and (2) of ecosystems according to the damage a future invader could inflict upon them. Applications can be developed with respect to prioritisation of species and habitats (in which to invest resources first?). For example, exotic species categorized as high-risk based on their traits, which spread close to vulnerable ecosystems (again: derived from traits), could be controlled first since greatest impact is expected. By combining the data with habitat preference of invaders, it could be assessed where high-risk invasive species have occupied suitable habitats and where not. Suitable, but at present invader-free, habitats should then get protection priority, especially for invaders with low habitat specificity. Species with highly specific habitat preference (e.g. *Rosa rugosa*, *Xanthium orientale*), should get lower priority at national level, though not necessarily in the region where they show strong invasive behaviour (e.g. sand dunes for *Rosa rugosa*). From the more specific findings of trait analysis, further recommendations can be drawn:

- Seed production was maximized by tall or productive species. Such invaders were characterized by low SLA and inefficient nutrient resorption, and occurred in dense, productive and nutrient-rich vegetation. Given the high explanatory power of these traits, they represent good candidates for prediction purposes.
- Dense communities, with limited light transmission, select for productive invaders, or stimulate invaders to grow taller. The absence of tall or productive invaders in unproductive ecosystems raised surprise, and some candidate mechanisms responsible for this are elevated wind speed (more resource investment required for mechanical support), greater warming and evaporation at ground level (higher drought risk during germination), higher light transmission (precluding dark germination), greater herbivory (due to less structural protection), … This finding suggests that management strategies that reduce biomass or productivity might be appropriate means to combat invaders (see also next point).
- Dense communities where large invaders were successful, were typically nutrient-rich. This may be a consequence of eutrophication, so combating eutrophication would be an effective strategy to limit invader success on a landscape scale. Intensely mowing invaded plots to remove nutrients from the ecosystem could also be a method for combating high-risk invaders. Removing the top layer, especially in case invaders induce nutrient uplift, is another possible strategy, though probably only of practical use for limited areas. Care should be taken, however, to avoid dispersing invader plant parts when plant material or soil is moved.
- Manganese (in soil, in invader tissues or uninvaded ecosystems) was always

negatively related to invader success. Low Mn may thus point at a high invasion risk, which is possibly related to soil pH or soil organic matter, and could therefore be considered for screening purposes.

- Certain characteristics of invaders were not included in this study. Vegetative reproduction for example, is a trait often related to success (e.g. in *Fallopia japonica* and *Solidago gigantea*), and should be taken into account when screening successful invaders.
- Beside success measures, also invader impact on ecosystems (soil changes) correlated with separate plant and separate ecosystem traits (joint analysis of UA and ULB data). Combining ecosystem and/or plant traits also for this variable may further improve our limited knowledge on the impact of alien plant invaders.

The impacts of alien invasive species on ecosystem processes and biogeochemical cycles might be of particular concern to management. In case ecosystem functioning is profoundly altered, the possibility to restore the initial vegetation could be strongly compromised. Our data show for the first time that ecosystem function is being modified by alien species invasion in Belgium.

The pattern of impacts on soil properties is largely species-specific and the 9 studied species can be categorized as follows:

- Increased availability of most elements in topsoil of invaded patches: this is the case of *Fallopia japonica*. For this species, alteration of topsoil chemistry is of particular concern to management. In particular, topsoil eutrophication may constraint vegetation restoration after removal of the invader.
- Limited impact on topsoil chemistry: *H. mantegazzianum* and *P. caeruleum*. For these species alteration of ecosystem function may not be of particular concern to management.
- Elevation of a single or only few nutrients. *Solidago gigantea* increases availability of P in topsoil.

Therefore, for a limited number of species, invasion may enhance ecosystem eutrophication and push invaded landscapes into a “eutrophication vortex”. For this reason, the preventive approach must be preferred to the curative approach. Since the impacts are species specific, new successful invaders will have to be assessed for their possible impacts. Future research should also be directed to detecting key traits of alien species that may be used as predictors of impact on ecosystems.

Another striking result is that impacts on soil are site-specific. Topsoil nutrient concentration is most often increased by invasive alien species in sites with the lowermost initial concentrations, while it is decreased in sites with the highest initial concentrations. In other words, invasive alien species tend to homogenise soil conditions at landscape scale. This is the first time, to our knowledge, that homogenisation effects of alien invasive species are demonstrated for soil properties.

These results raise new questions:

- What are the mechanisms of increased nutrient availability in topsoil under invasive species?.
- Alterations of N cycling need further investigations and be of particular importance to environmental issues (enhanced nitrification followed by nitrate leaching, …).
- It is of utmost importance to test if alteration of soil properties results in a positive feedback: are invasive plants more competitive in previously invaded soil.
- It has been proposed that alien species invasion may result in invasional meltdown, a process by which one invasive species facilitates subsequent invasion by other alien species. Alteration of topsoil chemistry may conceivably alter structure and composition of soil biota (microbial and animal communities) and this should certainly be examined.
- Finally, the existence of carry over effects (i.e. long–lasting soil alterations after removal of invasive alien species) must be formally tested by removal experiments. Such effects could make restoration difficult. It is therefore important to prioritise a preventive approach and to watch uninvaded sites to detect invasion at the very beginning of the process and eradicate the species before ecosystem functioning modification arises.

The analysis at the landscape scale testifies that invasive success is better explained by the quantity of suitable habitats in the landscape than by the seed ecology of the species. Crossing information on dispersal capacities, habitat selection and population monitoring would allow following the invasion dynamics at the landscape level, to predict which areas could be invaded in the future and, last but not least, to early localize new populations, when they are easiest to eradicate. Such an approach was beyond the scope of the current project. Monitoring consequently helps prioritising management actions. The results obtained for *Fallopia* spp., *H. mantegazzianum*, *I. glandulifera*, *S. inaequidens* and *Solidago gigantea / S. canadensis* demonstrated that roads and river banks are key elements for the invasion dynamics at the landscape scale. Consequently, management action plans have to be concentrated along roads and river banks.

Results also provide important information on species traits that would help to propose successful management solutions. The absence of a persistent seed bank in the soil for three major invasive species in Belgium, means that control of invasion may be achieved by eradicating populations. Specifically, populations monitoring in these two landscape units showed that *H. mantegazzianum* is at the beginning of its invasion. Considering the problems caused by this species in other countries (Mullerova et al., 2005) and the rate of increase in the studied landscape, management actions need to be planned urgently.

Human activities are important vectors (both directly and indirectly) in introduction and dispersal of alien species and more specifically invasive species. With its highly developed motor-, rail- and waterway network and as an important international trade centre, Belgium is prone to plant introductions. Despite its small surface, a remarkably high number of non-native plant species has been recorded in relatively recent times and this number seems to increase rapidly. Action plans should be developed to help preventing intentional and unintentional introductions for all relevant sectors in a participative fashion involving the main stakeholders, and they should address the main introduction pathways. Moreover, policies should be established with respect to early detection and control of detrimental non-native species. Adequate monitoring of non-native species has to be developed on the basis of the existing schemes. Although invasion biology is an expanding field in ecology worldwide, it has only recently begun to gain momentum in Belgium. Building up and maintaining scientific capacity is a prerequisite to success: scientists should be involved in the development of a national strategy concerning alien invasive plant species.

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SPSD II (2000-2005)

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