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Biology and ecology of an invasion of *Impatiens parviflora* DC in natural and semi-natural habitats

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Introduction

In recent decades since the publication of Charles Elton's book "Invasion by animals and plants" in 1958, we have been witnesses to the birth of a new branch of ecology – invasion science (Richardson, Pyšek 2008). The phenomenon of the introduction, spread and naturalisation of species of alien origin, called invasive alien species (IAS) in a new area is considered to be the second, after habitat loss, threat to native biodiversity (Wiliamson 1996; Weber 2003). Thus, besides botanists, zoologists and ecologists, invasions are receiving attention from naturalists, conservationists and practitioners in nature protection.

Ecologists and invasion biologists seek to answer the question of which species become invasive or potentially invasive (Williamson, Brown 1986; Weber 1997; Rejmánek *et al.* 2005) and what traits promote their invasiveness? (Baker 1965; Noble 1989; Rejmánek 1995, 1996; Jackowiak 1999). What are factors that control the vulnerability of habitats, plant communities and ecosystems to invasion, i.e., the so-called invasibility? (Tilman 1997; Lonsdale 1999; Davis *et al.* 2000). And finally, what is the impact of IAS on the native flora and fauna (Parker *et al.* 1999; Wilgen *et al.* 2001; Yurkonis, Meiners 2004)? The most important question, however, is how can we prevent and control IAS?

The body of literature related to biological invasions is enormous and therefore the terminology that is used to discuss biological invasions is very complex and often inconsistent. Authors use many terms to define invasive species and the processes of invasion. Thus, it is often stressed that this multiplicity of concepts and words can lead to misunderstandings. In addition to the term "alien", the species are referred to as "introduced", "acclimatized", "adventive", "invasive", "non-indigenous", "non-native", "allochthonous" or "exotic". Moreover, there are also such terms as "invader", "weed"(plant) and "pest"(animal), which reflect a more anthropocentric point of view than an ecological or biogeographical approach (Rejmánek 1995).

The following definitions were used for the purpose of the present study. All of them are definitions that have been agreed upon by the Convention on Biological Diversity (CBD) and then implemented in the "European Strategy on Invasive Alien Species" that was adopted by the Standing Committee of the Bern Convention. They are also used in the database "Alien species in Poland" at www.iop.krakow.pl/ias.

Alien species – a species, subspecies or lower taxon, introduced outside its natural past or present distribution; includes any part, gametes, seeds, eggs or propagules of such species that might survive and subsequently reproduce.

Invasive alien species (IAS) – an alien species whose introduction and/or spread threatens biological diversity.

Alien plants – plant taxa whose presence in a given area is due to the intentional or accidental introduction as a result of human activity. Practically, they are a subset of alien species that are plants, i.e. plant IAS.

Naturalized plants – alien plants that form sustainable populations year on year without the influence of humans.

Invasive plants – naturalized plants that produce a large number of offspring that may persist even at large distances from the parent plant. They can (not necessarily) threaten native biodiversity and/or human economy and/or human health.

Weeds – plants (not necessarily of an alien origin) that grow on sites where they are not wanted and that usually have detectable negative economic or environmental effects.

Introduction – the movement by human agency, indirect or direct, of an alien species outside of its natural range (past or present). This movement can either be within a country or between countries or areas beyond national jurisdictions.

Exotic range and **introduced range** – can justifiably be defined as the same. The exotic range is an area into which the species has spread due to human activity and from which it would otherwise be restricted from due to geographical barriers.

Native range – A region where a species naturally occurs without direct or indirect human interference. It is the area in which a species evolved or migrated without human help.

Invasion – The multi-stage process whereby an alien organism negotiates a series of potential barriers in the naturalization-invasion continuum. It begins with an introduction by humans, followed by naturalization and further spread. Invasion in this way is the same as **range expansion** but only in cases in which it concern alien species and human interference (Richardson *et al.* 2011) or **chorological expansion** *sensu* Jackowiak (1999). Originally, one of two variants of "ecological explosion" by Elton (1958), i.e. the introduction and spread in a new area corresponds to the present definition of invasion.

Taking into account the biogeographical-historical classifications of plants, the situation is even more complex which is shown in the dictionary of the synanthropization of vegetation by Sudnik-Wójcikowska and Kożniewska (1988). Many systems for the classification of synanthropic plants were developed in Europe, especially in the central part. The majority of them are adaptations of the Thellung system (Kowarik, Pyšek 2012). The terms that are used in Europe can be incomprehensible to people in other regions of the world. According to contemporary systems of classification, invasive alien plant species may be a subset of

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neophytes (=kenophytes in Poland) (Tokarska-Guzik 2005b; Tokarska-Guzik *et al*. 2012), i.e. alien species that were introduced after 1500. Those that are able to enter into (semi)natural plant communities are agriophytes, i.e. hemi- or holoagriophytes, respectively. Species that colonize man-made habitats and enter into ruderal and segetal plant communities are called epecophytes. Plants that are escapees from a cultivated area but that are not naturalized correspond to the term **ergasiophygophytes**, whereas casual weeds, i.e. species that have been introduced but that are not naturalized are **ephemerophytes**. Some authors have stressed that along the naturalization-invasion continuum plant species can be classified into different categories (Faliński 1998a).

There is no doubt that some species such as goldenrods *Solidago gigantea* and *S. candensis* as well as knotweeds like *Reynoutria (Fallopia) japonica*, *R. sachalinensis* and hybrid *R* x *bohemica* are true invasive taxa. In addition to their rapid range expansion, they have a negative impact on native (resident) plants in recipient communities. Their presence leads to a decrease in the species richness of phytocoenoses (e.g., Gerber *et al*. 2008; de Groot *et al*. 2011). Customarily or for practical reasons many alien plant species, especially those that were introduced after 1500, are treated as invasive taxa, although according to the CBD definition, not every species meets these criteria.

Small balsam *Impatiens parviflora* DC, which is native to East Asia, is among many species that have traditionally been regarded as invasive alien plant species. This plant, which was introduced into Europe in the 1830s, has been the subject of various types of research before. In 1956 the monographic paper about this species was published in the Journal of Ecology within the series Flora of the British Isles (Coombe 1956). Later, especially in the late 1950s and 1960s, small balsam was a model plant for ecophysiological studies (Causton *et al*. 1978; Evans, Coombe 1959; Evans, Hughes 1961; Hughes 1959, 1965abc, 1966; Hughes, Evans 1961, 1962ab, 1963, 1964; Elias, Causton 1975; Young 1981ab; Whitelam, Johnson 1982). In 1970s a set of papers that were chiefly devoted to the germination and seed ecology of small balsam were published (Jouret 1974ab, 1976, 1977ab). Finally, in 1984 a monograph about the history of its spread in Europe and a description of some of the phytogeographic, phytosociological and autecological aspects of the invasion *Impatiens parviflora* was published (Trepl 1984). Invasions by *Impatiens parviflora* in different geographical regions or countries were well-documented but unfortunately, some of them were not published in the form of papers despite presenting interesting and novel data about the ecology of the species, e.g., in Poland (Adamska-Wachowiak 1983; Kujawa-Pawlaczyk 1990; Budziszewska 2006; Dańko 2009; Jończyk 2007; Kozłowska 2013; Kraszewski 2007;

Michalik 2005; Piskorz 2004; Komosińska 2008; Lipińska 2011), Slovakia (Maćkova 2012, Tóthová 2011), the Czech Republic (Urban 2009), Hungary (Csiszar 2004), Belgium (Perez 2006; Vervoort 2011), Austria (Lemmerer 2010), Germany (Hertel 1994; Schaddach 2008). The problem of invasions was observed by governments, organisations, NGOs etc. Small balsam was listed and described in some online databases, e.g., CABI (Tanner 2008); NOBANIS (2013); European and Mediterranean Plant Protection Organisation (EPPO) (EPPO…2011). The majority of the papers that are concerned with or that mention small balsam present floristic and phytosociological studies.. Purely autecological papers or works in terms of community ecology research that focus on *I. parviflora* as the main object of study are rarer. One of the first examples that showed its distribution and presence in plant communities in a large geographical region, Pomerania, was the work by Ćwikliński (1978). Case studies from the Primeval Białowieża Forest were conducted by Adamska-Wachowiak (1983), Kujawa-Pawlaczyk (1990,1991) and Adamowski and Keczyński (1998). The process of the invasion of small balsam in this large forest complex was described in those works. Synecological studies on permanent study plots in various forest communities in a chosen forest nature reserve (Warsaw) were performed by Obidziński and Symonides (2000). As a result of research in the Wielkopolski National Park, a series of autoecological and biocenotical papers by Klimko and Piskorz 2003; Klimko *et al.* 2009; Piskorz 2005; Piskorz and Klimko 2001, 2002, 2006, 2007; and Piskorz and Urbańska 2007 were published. Both an autoecological and genetic study were conducted by Komosińska *et al.* (2006). Several phytosociological surveys have been done in the Silesian Upland and the Jurassic Upland, which are situated in southern Poland, (Chmura, Orczewska 2004; Chmura, Urbisz 2005; Chmura, Sierka 2007). Autoecological studies (Chmura *et al.* 2007) and studies on permanent study plots (Chmura and Sierka 2006ab; Sierka et al. 2009) have also been done. In addition, an interdisciplinary autoecological-mycorrhizal study was performed by Chmura and Gucwa-Przepióra (2012).

The enormous body of literature on this plant is very often ambiguous on this topic and often presents conflicting data. This reflects the differences in the specificity of the regions that are studied, the history of invasions and the methods that are applied rather than the general patterns of the invasiveness of small balsam. In spite of this some, review publications on *Impatiens parviflora*, including one monograph (Coombe 1956; Trepl 1984; Eliáš 1999) and more recently a monographic paper (Csiszar, Bartha 2008) that were published did not explore or fully explain all aspects of the ecology of this plant. Hopefully, this work will contribute to the knowledge about the ecology of small balsam. The main goal of this

publication is to summarise and discuss the mechanisms of invasion by *Impatiens parviflora* on the basis of the author's own research and other authors' earlier studies.

Main aims and hypotheses

I. parviflora can be regarded as a "true" invader species because it was introduced unintentionally. Since its establishment, the processes of naturalisation and its further spread have been spontaneous. Small balsam has been successfully established in seminatural and natural habitats, i.e., forest margins and forests. This plant very frequently found in protected areas. It occurs in 22 of the 23 national parks and in the majority of landscape parks in Poland (Najberek, Solarz 2011). Moreover, observed lag of phase during its invasion history makes the species more interesting. The majority of the research presented in this work was done in the field in well-preserved or only slightly disturbed forest communities. Most of the study plots are situated in nature reserves and more rarely in managed forests. The knowledge about species behaviour in natural and semi-natural communities for the purpose of the present study is the most important and does matter a great deal from a nature conservation viewpoint. The observations that are presented and the results of the fieldwork in a spatial and temporal design are related to other, interesting studies that were conducted in greenhouses, laboratories and in field experiments.

The main objective of the work is to estimate to what extent the success of an invasion of *I. parviflora* is dependent on the invasiveness of the species, i.e., the set of biological (determined by genetic factors) and/or on ecological characters (determined chiefly by environmental factors) and on the environment in the sense of the intrinsic factors of the habitat that make it vulnerable to an invasion, i.e., invasibility. Both the phenomena and the terms by which they are described are difficult to separate because they partially overlap.

Based on the literature that is available, the research of the author and others and the different patterns in invasions of *I. parviflora* that have been observed, the following detailed questions were posed and particular hypotheses that were related to them were formulated:

- Are there any relationships between the edaphic conditions and the abundance of *I. parviflora*?

H_0: The abundance of *I. parviflora* increases with an increase in the content of nitrogen, phosphorus and potassium.

H_1: The abundance of *I. parviflora* does not depend on the edaphic conditions but on the disturbances of habitats.

- If the morphological plasticity of *I. parviflora* is dependent on the soil parameters, then how are variations in selected plant traits affected by the type of forest community?

H_0: The morphometric traits, phenology and germination ability vary significantly among forest communities under the tree canopy in forest interiors.

H_1: The morphometric traits, phenology and germination ability differ significantly only from individuals growing on forest paths/forest margins.

- Was the synergic effect of light availability and the high content of nutrients studied in lab conditions on the morphological plasticity of *I. parviflora* that is known from literature (Peace, Grubb 1982) observed in field conditions? Do the canopy openings and the nutrients of decaying dead wood enhance plant fecundity? Does a natural disturbance favor some phenotypes and lead to persistence in the forest interior?

H_0: The size of individuals is biggest on sites near decaying dead logs where the soil is affected by the decomposition of dead wood and under canopy openings.

H_1: Only light availability has an impact on the size of individuals of *I. parviflora*.

- How does the invasiveness of the species change among various microhabitats? Which microhabitats are occupied by individuals that are characterised by a large size and a higher number of flowers and fruits?

H_0: Disturbed habitats (forest paths and margins) are characterised by a massive presence of large and fecund individuals of *I. parviflora*. Other microhabitats do not play an important role in the spread and persistence of the species.

H_1: In addition to forest paths/forest margins and the soil under the tree canopy, there are other microhabitats (associated with dead wood complex) that are frequently colonised by *I. parviflora* where it is able to grow and finally set seeds.

- What is the temporal variation of the occurrence of *I. parviflora*? Under which conditions does the abundance of the species change? Which natural and anthropogenic factors determine an increase in abundance? As an annual does small balsam establish the same places using old and new gaps in the forest layer? To what extent is this process determined by its earlier presence or is a random?

H_0: Small balsam is invasive species; thus it increases in abundance over time.

H_1: The dynamics of small balsam are random or depend on many factors that are hard to predict.

- What is the role of arbuscular mycorrhiza (AM) in *I. parviflora*? What abiotic factors have an impact on it? How does AM influence the size and fecundity of the species?

H_0: The abiotic factors that occur in particular plant communities are manifested in the presence/absence of AM in *I. parviflora*. The size of plants and their fecundity are first of all correlated with the frequency of mycorrhiza followed by other arbuscular mycorrhiza indices.

H_1: Abiotic factors mainly have an impact on the values of the AM colonisation indices. Forest plant communities do not differ in the presence of AM+ plants. The size of plants and the fecundity of *I. parviflora* depend on various traits of mycorrhiza colonisation.

- What is the role of functional plant groups in relations with *I. parviflora*? Which plant functional group is displaced or affects the presence/abundance of small balsam?

H_0: There are some plant functional groups whose representatives have a higher cover in uninvaded sites when compared to sites that have been invaded by *I. parviflora*. The species of some plant functional groups are able to displace *I. parviflora*.

H_1: The contribution of particular plant functional groups does not matter in the absence/presence of *I. parviflora*.

- Does *I. parviflora* colonise "empty sites" *sensu* Harper (Tilman 1997) in forest communities? Is the naturalisation of *I. parviflora* an effect of the displacement of native species due to its competitive ability? Does the cover of native and resident species have an influence on the abundance of *I. parviflora*? If yes, how does this impact change among various forest types?

H_0: There are some species that are affected by *I. parviflora* and they can be hindered or displaced by the species. Then, the species meets criteria of invasiveness according to definition by Convention on Biological Diversity.

H_1: No, *I. parviflora* prefers sites where there is bare soil or a lower species richness and cover of native plants. In species rich communities, it is displaced by them.

1. The object of the study: *Impatiens parviflora*

1.1. Characteristics of the species

1.1.1. Taxonomy

I. parviflora DC, was described by De Candolle in 1824 (Coombe 1956). The synonym name is *Impatiens nevskii* Pobed. It belongs to the family *Balsaminaceae*. According to various sources, the genus *Impatien*s is estimated to contain from about 850 (Csiszar, Bartha 2008) to more than 1000 species (Janssens *et al.* 2006). As a result of molecular phylogenetic studies, *Balsaminaceae* was reclassified as a family in the *Ericales* (an order of 26 families) sitting as a sister group to all of the other *Ericales* in the Balsaminoid *Ericales*. The Balsaminoid *Ericales* consists of the families *Balsaminaceae, Marcgraviaceae, Pellicieraceae* and *Tetrameristaceae*. Together this group comprises approximately 1130 species (Tanner 2008). Based on molecular evidence, it can be concluded that *Impatiens parviflora* evolved ca. one million years ago – in the mid Pleistocene and its most nearly related congener species is *I. balfourii*. A probable ancestor of small balsam originated from southwestern China (Janssens *et al.* 2009). An older taxonomical classification indicated that *I. parviflora* belonged to the *Brachycentron* section and *Micropetalae* series inside the *Cauliimpatiens* subgenus (Jørgensen 1927 after Csiszar, Bartha 2008). Nowadays, *I. parviflora* is a representative of one of the 15 clades within the genus *Impatiens* together with, among others, *I. glandulifera* and *I noli-tangere* (Janssens *et al.* 2006). Below is the taxonomic classification of small balsam (Tanner 2008).

Domain: *Eukaryota*
Kingdom: *Plantae*
Phylum: *Spermatophyta*
Subphylum: *Angiospermae*
Class: *Dicotyledonae*
Order: *Balsaminales*
Family: *Balsaminaceae*
Genus: *Impatiens*
Species: *Impatiens parviflora*

1.1.2. Morphology

Small balsam is a glabrous annual herb that is usually 20-60 cm tall, but which can also be as short as 4 cm (Chmura 2008a). Rarely it reaches 150 cm (Coombe 1956) and even taller – 152 cm (Chmura 2008a), 165 cm (Chmura npbl) and ca. 170 cm (Adamowski personal com). The tallest recorded plant was 205 cm (Dańko 2009). The root system is shallow with a short-lived primary root that is supplemented by growing stronger lateral and adventitious

roots from the lower node (Hegi 1965; Coombe 1956; Sebald *et al.* 1998; Csiszar, Bartha 2008). The adventitious roots sometimes develop on the aboveground part of plants. The plant is single stemmed or branched from the lower nodes with third-order branches in well-developed plants that grow under favourable conditions in terms of habitat fertility and a medium density of population (Coombe 1956; Chmura npbl). The leaves are simple, alternate, ovate, elliptic or wide-lanceolate and are usually 5-12 cm long and 2.5-5 cm wide and sharply serrated at the edges with 13-35 teeth on each side (Tanner 2008). Petioles carry stalked glands that may serve as extrafloral nectaries. The length of the petioles gradually decreases with the height of the stem. In the lowest part, they can be as long as four cm but on the upper part they are only about 0.5 cm. Zygomorphic flowers are located in inflorescences, which are axillary racemes. An inflorescence bears from (1-) 4-10 to (-15) flowers. Racemes are as long as the upper leaves or longer. The flowers are 10-15 mm long including their spur and upright. The corolla is pale yellow with red spots on the inside but white flowers with yellow patterns have also been described. There are five sepals, the two frontal ones are reduced, the two lateral ones are rudimentary green and about three mm long (Csiszar, Bartha 2008). The back sepal forms a straight spur that is 5-10 mm in length and has the same colour as the petals. The lateral and back petals of corolla are in pairs; the frontal petal is large (up to 10 mm long). Five stamens stand alternately with the petals inside the flower; the filaments grow freely and the anthers stand together. Five carpels form the pistil and the ovary is superior. The fruit is a capsule that is linear to club-shaped, 15-25 mm long, glabrous and green. The brown coloured seeds are 3-5 mm long with one to five fine longitudinal striations per capsule (Csiszar, Bartha 2008; Tanner 2008). Records for the *I. parviflora* seed mass vary from 6.91 to 9 g per thousand seeds according to the database of Royal Botanic Gardens, Kew (RBG 2008) but according to Moravcová *et al.* (2010), the mass of 25 propagules (g), which are probably seeds, is 0.1422±0.0135. The mean length of a propagule (seed) is 4.01±0.34 mm and the width is estimated at 1.97±0.29 mm.

1.1.3. Biology

Variablity and molecular biology

It is commonly assumed that there is little genetic variation in the invasive populations as compared to the native ones. Two forms are known in Europe – varietas *albiflora* with white flowers, yellow spots inside and the forma *albescens* that has white flowers with orange spots in the throat of the flower (Jørgensen 1927). Some initial reports about the genetic variability of the species in Europe that were performed in Poland (Komosińska *et al.* 2006)

and in Lithuania (Janulionienė *et al.* 2011; Kupcinskiene *et al.* 2013b) shed some light on this problem. In the latter study, it was revealed that those genetic distances among populations are correlated with geographical distances. In the former, smaller study conducted in Poland, no genetic differences between the two populations were detected; however, a common gardens experiment suggests little genetic differences. Kupcinskiene *et al.* (2013b) demonstrated that multiple introductions occurred in Lithuania, and therefore it can be assumed that a similar phenomenon took place in other parts of Europe. The chromosome numbers that were recorded are 2n=20, 2n=24 and 2n=26. No hybrids are known in Europe (Coombe 1956); however, it can coexist with *I. noli-tangere*, which is native to Europe and more frequently with another alien species, *I. glandulifera*, in an adventive range.

Phenology and physiology

I. parviflora plants in Europe usually germinate in late March or April. The time from germination to flowering is eight to nine weeks with the seeds ripening three to four weeks later (Coombe 1956). Flowering usually begins in May or June and lasts until late September or mid-October with the oldest recorded plants being seven months old. The phenology of the plants differs depending on the types of habitats in terms of aspect, light availability and disturbance (Chmura 2008ab; Piskorz, Klimko 2002; Piskorz 2005). The species is autoperiodic, i.e., it can grow from seed to fruit at any time of the year in a greenhouse under suitable conditions of seed dormancy and germination (Coombe 1956). A series of field and laboratory experiments (Evans, Hughes 1961; Hughes 1959, 1965abc, 1966; Hughes, Evans 1961, 1962ab, 1963, 1964) revealed some patterns of the plant's physiological response to environmental factors with regard to its seasonal cycle and daily balance. It was confirmed that the minimum period of dormancy after ripening is 90 days in wet conditions and 5° C. During growth, the hypocotyl increases with a decreasing light intensity and a higher temperature in red light. A low temperature and blue light as well as a greater vapour pressure deficit and a higher nutrient status are typical for shorter hypocotyls. Under natural conditions in the field, such a situation enhances the development of adventitious roots in cases in which the hypocotyls are too long and too weak to support the growth of plant. The distribution of the total dry weight and biomass allocation of small balsam is affected by many factors (Hughes 1965; Eliaš 1992). The unit leaf rate is proportional to daylength at a high light intensity. The quantum efficiency for apparent photosynthesis is almost identical in blue and red light and it appears to be optimum at 15° C. The unit leaf area decreases with increasing plant size. A high nutrient status reduces the specific leaf area, whereas blue light and an

increasing plant size reduce both the specific leaf area and leaf weight ratio. A low temperature reduces the specific leaf area but does not influence the leaf weight ratio, which matters in early spring and limits the growth of plants in field conditions. The highest rate of increase in leaf area takes place in spring and early summer at 10% of the daylight factor (Hughes 1965). Whitelam and Johnsson (1982) observed a response of nitrate reductase activity to simulated canopy radiation of a low photon influence, which characterises the light conditions in shade. Small balsam showed a marked and rapid response to changes in the photochrome photoequilbrium with low-fluence rate sources. The authors explain the ability of *Impatiens parviflora* to display strong responses to added red light by its ability to tolerate much reduced fluence rates of PAR (photosynthetically active radiation), which is often found in natural habitats. Thus, this clarifies why small balsam can grow both in very deep shade and more open habitats. Ugoletti *et al.* (2011) studied 18 ecophysiological traits in three alien *Impatiens* species including *I. parviflora*. These were, among others, traits associated with plant growth and allometry, reproductive capacity and leaf physiology. In the beginning the plants were reared in pods in a greenhouse and later were moved outside to an open area. The maximum growth in these plants was observed at the end of August and amounted to an average ± SE of 1.48 ± 0.25cm per a day. The leaf weight ratio (LWR) was 0.299±0.047 (mean ± SE), leaf area (LAR) was 0.0065± 0.0004 (mean ± SE), stem weight ratio (SWR) was ca. 0.6 of g stem g^{-1} plant and specific leaf area (SLA) was 0.025 m^2g^{-1} leaf. The mean percentage of water in fresh mass, which reaches as much as 92%, is one of the highest amongst herbaceous plants (Drobnik 2007). Small balsam is listed as an ozone-sensitive plant and is often the subject of studies that are focused on the impact of ozone on the condition of plants (Godzik 1996; Bergmann *et al.* 1999; Skelly *et al.* 1999; Manning *et al.* 2002; Manning, Godzik 2004).

Reproductive biology

Small balsam is an annual plant, i.e., a therophyte. Propagation is entirely by seed. Capsules can contain from one to five seeds. The flowers are protandrous with a male phase of two to four hours and a female phase of one to two days (Tanner 2008). Flowers can be cleistogamous although chasmogamous ones are much more common. Flowers are visited mainly by insects from the *Syrphidae* family of which 19 species were found on *I. parviflora* (Schmitz 1998). All flowers usually set seeds independent of the intensity of insect visitation. The plant is self-compatible, geitonogamous and allogamous pollination results in no differences in a set of seeds. The most fecund individuals can produce 1000-2000 per plant

(Trepl 1984); however, Coombe (1956) estimated a maximum amount of 10,000 seeds. In an alder forest a single plant had 90 seeds on average while a single plant had only 10-30 seeds in hornbeam-oak forests (Trepl 1984). According to Moravcová *et al.* (2010), the average number of propagules is 279 per single plant and 2689 per $1m^2$ (in the maximum population density found in a locality). Many authors have conducted germination experiments and have obtained different results because of various storage conditions. Seeds require low temperatures to break dormancy but temperatures below -20° C kill all seeds (Coombe 1956). Kinzel (1927) found that at room temperature none of seeds germinate but with seeds stored at -5° C, the germination rate was 100%. A surprising result was obtained by Coombe (1956) who after three days of an experiment (+5C, wet) noted 100% germination. According to Jouret (1974ab) temperatures between 0° C and 5° C are ideal for germination. The shortest stratification period that results in germination is 13 days. The duration of the stratification has an influence on the increase in the germination rate. Seeds remain viable for less than three years when they are stored dry at room temperature but they still germinated after four years when kept in wet conditions (Coombe 1956). Burying seeds delays the time of germination slightly (Schaddach 2008). Opinions about seed banks of *I. parviflora* are contradictory. Csontos (1986) in a removal experiment suggested the existence of seed banks. Two years after seeds were put into the soil 14% of the previous population regenerated. During the time there was no seed output from neighbourhood. According to Perglová *et al.* (2009), only alien *I. capensis* and native *I. noli-tangere* form short-term persistent seed banks. The native balsam was known from the existence of seed banks from many earlier studies (e.g., Pirożnikow 1983; Falińska 1990).

1.1.4. Habitats

   I. parviflora is a species that grows on a wide range of mineral soils with a pH range in the rhizosphere from 4.5 to 7.6 in UK (Coombe 1956). The species has been found in heavily acidic sites (pH= 4.12) (Csiszar, Bartha 2008) in Hungary and even those with a little less (pH<4.1) in Poland (Chmura et al. 2007). Most soils are brown soils or rendzinas and the plant avoids waterlogged conditions (Coombe 1956). The species has also been encountered in alkaline soil in calcareous grassland (Chmura 2008a). Small balsam showed a positive response measured as an increase of the percent of cover to the compactness of soil (Godefroid, Koedam 2004a). It is a temperate species that prefers shade and half-shade and is mostly found in 5-40% relative daylight (Tanner 2008). According to Borhidi (1999), while

small balsam is plant of shade or half-shade, it can also survive on open sites. Survival in open habitats is influenced by the moisture of the stratum (Coombe 1956).

It mainly penetrates forests that are under a strong human influence, such as managed forests and timber plantations, as well as natural old-growth forest types. It is found more often in moist to wet forests from floodplains, alder forests mad beech forests rather than in mixed or coniferous forests. In addition, the species occurs in the ruderal vegetation in settlements, mainly on roadsides and in gardens. Human disturbance in forest habitats generally promotes the spread of *I. parviflora* (Trepl 1984; Eliáš 1999; Csiszar, Bartha 2008); however, fire has a negative impact. Comparison of the flora from burnt and unburnt sites indicates that the species avoids former burnt sites (Maringer *et al*. 2012).

Taking into account the number of types of habitats small balsam is to be found in a wide range of biotopes. According to the European Nature Information System (EUNIS) classification *I. parviflora* grows in 68% of 33 main types of habitats (Chytrý *et al*. 2008), whereas in more detailed classification which corresponds to phytosociological alliances or groups of alliances amounting in a total of 68 types (Sádlo *et al*. 2007) *I. parviflora* was recorded in 45 types (Pyšek *et al*. 2012). On the basis of comparison with other neophytes and invasive species it turned out that small balsam is one of the species with the widest ecological amplitude.

1.1.5. Biotic interactions

Associated plant species

In Trepl's opinion (1984) *I. parviflora* occurs frequently in seven phytosociological classes and 20 alliances in Central Europe; however, the range of vegetation units where it is present is wider. These are mostly deciduous forests (*Querco-Fagetea* class), i.e., oak-hornbeam forests (*Carpinion betuli*) consisting in *Quercus* spp, *Carpinus betulus, Tilia cordata, Acer pseudoplatanus*, *Acer platanoides*, beech woods (*Fagion sylvaticae*), floodplain forests (*Alnenion glutinosae-incanae, Ulmenion minoris*) and alder and willow carrs (*Alnetea glutinosae* class) with *Alnus glutinosa*. It also occurs in mixed and coniferous forests (*Vaccinio-Piceetea* class) and plantations under *Pinus sylvestris, Picea abies, Abies alba, Larix decidua* etc. The species can also be found in acidophilus oak forests (*Quercetea robori-petraeae*) and can grow in scrub communities (*Rhamno-Prunetea*). It usually occupies disturbed sites in forests, e.g., forest paths and forest edges. In forest interiors it can grow on sites that are not favourable for other herbaceous plants because of low light levels, heavy competition by tree roots or thick litter layers. In nitrophilous forest edges and eutrophicated

forests, it is associated with *Geranium robertianum, Geum urbanum, Chaerophyllum temulum, Alliaria petiolata, Chamaenerion angustifolium*, which are mainly representatives of the *Epilobietea angustifolii* class (Trepl 1984; Schmitz 1998; Kowarik 2003; Tanner 2008). There are reports about massive or quite abundant occurrences of small balsam in other types of vegetation, e.g., chasmophytic vegetation, i.e., vegetation of rocks – the *Asplenietea Trichomanis* class (Anioł-Kwiatkowska, Świerkosz 1992; Świerkosz *et al.* 2011) and post-bog meadows on habitats of fens and transitional mires (the *Scheuchzerio-Caricetea fuscae* class) (Podlaska 2010). Small balsam occurs very rarely in natural patches of fens and bogs and grows only in drainage and disturbed parts of these types of vegetation (Sadowska 2011). It was reported that small balsam can occur in arable fields including crop fields (wheat, rye, sugar beets, oilseed rape and maize), but the plants were chiefly found in the shaded edges of fields along the shrub and tree zones (Dajdok, Wuczyński 2008).

The anthropogenic, ruderals, habitats that are occupied by the species include parks, cemeteries, garden allotments, wastelands, cottage yards, refuse tips and railway tracks and embankments (Tokarska-Guzik 2005a, Ciosek, Bzdon 2003; Faliński 1966; Klimko, Bozio 2003; Sowa, Warcholińska 1980; Szmajda 1974; Załuski 1974; Celka, Żywica 1994; Warcholińska 2005; Rostański 2006). Small balsam is a characteristic species for the *Alliarion* alliance (Matuszkiewicz 2011) and sometimes the plant association *Impatientum parviflorae*, which occurs in ruderal habitats, is distinguished (Brzeg, Wojterska 2001; Wika *et al.* 2002).

Associated fungi species

No mycorrhiza were known until the beginning of the 1950s (Coombe 1956) and this information was copied and cited in many further publications (e.g., Tanner 2008). Probably Truszkowska (1953) was the first who provided information about arbuscular mycorrhiza in *I. parviflora* among other species in floodplain forests. Others who mentioned mycorrhizal fungi in small balsam were Peace and Grubb (1982) who were later cited by (Harley, Harley 1987; Wang, Qiu 2006). In 2009 species gained the definite status of a mycorrhizal species (Štajerová *et al.* 2009).

Five phytopathogenous fungi were found on *I. parviflora*: (*Shaerotheca balsaminae*, order *Erysiphales*) *Aschyta impatiensis, Phyllosticta impatientis* from *Sphaeropsidales* and two rust fungi (*Puccinia argentea, P. komarovii*) (Schmitz 1998; Csiszar, Bartha 2008). The rust *Puccinia komarovii* is one the greatest enemies of small balsam, which can cause mortality that can even reach 100% (Eliáš 1995; Bacigálová *et al.* 1999). This species was brought from

Central Asia, which is the native region of *I. parviflora*. Its westward spread has been observed since 1921 when it was first found in the Ukraine (Kiev), in Germany in 1935, Switzerland in 1938, Slovakia in 1942 and still continues ever westward. The first record of this fungus in Poland was in 1934 (Trepl 1984; Majewski 1979). Piskorz and Klimko (2006) studied the impact of this rust on the population of small balsam in detail and demonstrated that infected populations differ from healthy ones in the seasonal dynamics of changes in abundance; high mortality is observed as early as May and the first part of June; the infection and its intensity stimulates the growth of the stem and the hypocotyls and fresh weight of infected plants is about 30% less than the weight of uninfected plants but the weight of the generative organs decreases significantly by more than 50% in some cases. The rust infection also affects reproduction efforts, which is expressed by the ratio of the weight of the fruits (or only seeds) to the total biomass, which shows a distinct downward trend. Other pathogenic fungi that can be encountered on the seeds of small balsam are *Rhizopus stolonifer, Rhizopus oryzae* and *Absidia glauca*; however, they occur more frequently on native *I. noli-tangere* (Budziszewska 2006).

Pathogenous arthropods and flower visitors

Schmitz (1998) mentioned 13 phytophagous species that consume small balsam. Among them there are 12 insect taxa. Eight are polyphagous taxa: *Sminthuridae* sp of *Colembola* order, *Anthropophora alni, Philaneus spumarius, Aphis fabae cirsiiacanthoidis*, *Aphis nasturtii* of *Homoptera*. *Lygus* spp (e.g., *Lygus pabulinus*) from *Heteroptera* and two species of *Lepidoptera*: *Xanthorhoe birivata* and *Pergesa elpenor*. There are also two monophagous species of the 2nd order – aphid *Impatientinum asiaticum* and from the *Diptera* order – *Phytoliriomyza melampyga*. The former species is native to Central Asia and followed its host plant but was introduced later; probably more than 100 years later (Schmitz 1998; Eliašova 2011). It can also be found on *Impatiens glandulifera*; however, it has not been noted on *Impatiens noli-tangere*, which is native to Europe yet. It cannot be excluded that the distribution will continue to the native congener (Ripka, Csiszar 2008). The leaf-mining fly *P. melampyga* (=*Liriomyza impatiensis* – previous synonym) was already described by Vogel (1943) after Csiszar, Bartha (2008) and Coombe (1956). Aphids are the dominant group. As Csiszar and Bartha (2008) reported, ca. 94% of all individuals found belonged to this group of insects. Aphids were present on the 74% of all of the investigated plants.

Hoverflies (*Syrphidae* family) are the most important group from among flower visitors. In total 19 species and their larvae were recorded on small balsam. They play the role of

pollinating species because hoverflies collect nectar and pollen from the flowers (Csiszar, Bartha 2008). Perhaps one of the reasons that hoverflies are attracted to the flowers of *I. parviflora* is their colour, which is especially favoured by this group of insects (Lunau, Maier 1995; Arnold *et al.* 2009). Schmitz (1998) lists 14 species as among those that are true pollinators, e.g., *Melanostoma mellinum, Scaeva pyrastri, Sphengia clumpe*. Rich aphidophagous fauna is associated with the aphids that are present on *I. parviflora*. Four species of hoverflies are both pollinators and aphidophagous in the larva that feed on *Impatientum asiaticum*, e.g., *Bacca elongate*. The remaining three hoverflies species are exclusively aphidophagous insects. They are usually attracted by dense colonies of *Impatientinum asiaticum*. Other representatives of this group are species from *Heteroptera* (three species), *Coccinellidae* (four species), *Neuropteroidea* (five species), *Sphecidae* (two species) and two other parasitoid aphid species. When compared to *I. noli-tangere* and *I. glandulifera*, the most aphidophagous species are on small balsam, while in turn, the lowest number of phytophagous species was found on them but they were more abundant. Small balsam does not have well-developed extrafloral nectarines like *I. glandulifera* and *I. noli-tangere*, and therefore the species richness of extrafloral visitors is the lowest (Csiszar, Bartha 2008). One of the reasons for the relatively small number of pollinators is its low nectar secretion compared to the two congeners mentioned above (Vervoort *et al.* 2011). Najberek et al. (in preparation) confirmed that among arthropods aphids are the most important group followed by representatives of *Diptera, Hymenoptera, Coleoptera*. The representatives of the *Hymenoptera* order, i.e., *Bombus* spp., which fly from flower to flower, were observed in both Poland and Hungary (Csontos, Chmura unpublished). Representatives of *Apidae* (*Bombus* spp, *Apis melilifera*) can also be found on two other congeners – *I. glandulifera* and *I. noli-tangere* (Vervoort *et al.* 2011). Small balsam plants are also visited by ants (*Formicidae*) and spiders. The first group is attracted by the aphids, which provide honey-dew and the latter group are predators (representatives of four families – *Linyphiidae, Aegelnidae, Thomisidae* and *Clubionidae*) (Csiszar, Bartha 2008). The species composition of arachnofauna does not differ from the fauna of spiders that visit other herbaceous plants in the neighbourhood. Two species of *Acari, Anystidae sp* and *Trombidiidae,* are parasites of aphids (Schmitz 1998).

Other invertebrates

Schmitz (1998) listed one snail species, the grove snail (*Cepaea* sp) of *Helicidae* family, which feeds on the leaves of small balsam. It is native to Western and Central Europe but is

invasive in North America. Piskorz and Urbańska (2007) observed *Columella edentula* on leaves in an oak-hornbeam forest. It was revealed that *I. parviflora* was used as food for the snail and as a protection from predators and direct sunlight. The leaves of small balsam under which the snails occurred provided stable humidity as well. What is important is that a comparison of seasonal variations and abundances with other species that were present in the herb layer showed that *I. parviflora* was most frequently colonised by *C. edentula*.

Vertebrates

It is rarely grazed by herbivorous mammals. Only roe deer, *Capreolus capreolus*, was reported to feed on the shoots of this plant; animals other than the deer avoid this species when compared to *I. noli-tangere* (Schmitz 1998). Rabbits, *Oryctolagus cuniculus* and other forest mammals such as rodents do not feed on this plant (Coombe 1956).

Allelopathy

Several studies have showed that small balsam is an allelopathic plant (Vrchotová *et al*. 2009; Csiszar, Bartha 2008; Csiszar *et al*. 2012). In these studies other methods were used but they revealed that under laboratory conditions *I. parviflora* had intermediate inhibitory effects after *I. glandulifera*. Vrchotová *et al*. (2009) tested the effect of water, methanol and dichloromethane extracts from the leaves of three *Impatiens* (*I. noli-tangere*, *I. parviflora*, *I. glandulifera*) on the germination of the seeds of two model plants – *Leucosinapis alba* and *Brassica napus*. All of the tested extracts had inhibitory effects on the seeds of all of the plants studied (except for the dichloromethane extracts).

The extracts from *I. parviflora* inhibited both the percentage of germination and the lengths of the radicle and hypocotyl in the germinated seeds of the plants studied. Csiszar and Bartha (2008) proved that mustard seeds (*Sinapis alba*) that are treated with a 5 g/100 ml concentration extract differed considerably from the control (only 86.66% of the seeds germinated). In another laboratory study, Csiszar *et al*. (2012) used the juglone index, which is based on comparing the effects of treatment with 1 mM juglone and a substance that is extracted from a plant species with an unknown allelopathic potential. The juglone index is the quotient that is created by the germination rate, shoot length and root length of white mustard (*Sinapis alba* L.) that has been treated with juglone and a substance from a potentially allelopathic plant. According to that study, small balsam at both lower and higher concentrations, i.e., 1- and 5 g plant material/100 ml distilled water revealed an inhibitory effect. The index scored 1.05 and 1.17, respectively. Among 14 herbaceous and 20

woody species, the juglone index for a lower concentration of *I. parviflora* was second after *Amorpha fruticosa* (1.11) and the seventh one (*Phytolacca esculenta* – the highest 5.49) for a higher concentration. *I. parviflora* has a repellent and toxic effect on some insects (Pavela *et al.* 2009). During an experiment with three *Impatiens* species (including *I. noli-tangere* and *I. glandulifera* as well) and their influence on *Myzus persicae* (aphid, *Homoptera*) was demonstrated. *M. persicae* (green peach aphid) is an important pest for many plants. After 54 h of exposure, the most active extract was *Impatiens parviflora* with a 99.7 and 90.0 % mortality at concentrations of 0.5 and 0.1 %, respectively and with high percentage of repellency (90-100%) at different times (from five to 48 h). The extract of *I. parviflora* contained tryptophan (2.13 mg/g); 2-methoxy-1,4-naphthoquinone (0.02 mg/g), total flavone (7.64 mg/g) and total derivatives of caffeic acid (15.60 mg/g). The authors believe that the plant can be used as an insecticide.

1.2. History of invasion

1.2.1. History of spread in alien range

Native range

The native range of *I. parviflora* encompasses the mountains of central Asia. According to Trepl (1984), there are parts of the range that consist of scattered areas in which the species is interspersed with areas without it in countries such as Turkmenistan, Afghanistan, Turkmenistan and Mongolia (Trepl 1984). The USDA-ARS (2008) database indicates part of central Asia, including Kazakhstan, Kyrgystan and Uzbekistan, also Xinjiang, China as its native range. Other parts of Asia, i.e., the Russian Far East are treated as a naturalised range. *I. parviflora* occurs along rivers and streams, in shady and humid localities in parts of the former USSR (Komarov 1934-1964 after Obidziński, Symonides 2000). In areas with steppe or semi-desert vegetation, the species can only occur in more humid forest patches, e.g., in floodplains or on northern slopes (Tanner 2008).

Spread in an alien range

Apart from Europe the alien range also includes East Asia, Western and Northeastern America (Adamowski 2008). The history of its introduction into Europe was described in detail by Trepl (1984), who gave the approximate dates of its introduction for all of the countries where small balsam is now present. The putative first record of the introduction of *I. parviflora* is often estimated to be around 1830 or shortly before that date (Trepl 1984;

Galera, Sudnik-Wójcikowska 2010) or in 1831 (Coombe 1956; Trepl 1984). Its seeds were then introduced into the botanical garden in Geneva (Switzerland) on purpose for cultivation. The first naturalised stand (in the wild) in the neighbourhood of the above-mentioned botanical garden was reported in 1831 (Coombe 1956); however, according to De Candolle (after Höck 1900 after Trepl 1984), the first date of a naturalised record was 1837. In turn, Probst (1949) after (Trepl 1984) indicated Solothurn, which is also in Switzerland, as the first naturalised locality. The online atlas of British & Irish Flora indicates 1823 as the date of introduction (BRC 2008). This is probably an error. Galera and Sudnik-Wójcikowska (2010) analysed the migration history of the species whose introduction was associated with botanical gardens at the beginning of the early stages of invasion. Based on their studies, it was noted that *I. parviflora* had 46 historical records from 30 European botanical gardens as an escapee. The next known naturalised stand dates back to 1842 in Dresden five years after its introduction into the town's botanical garden in 1837 (Trepl 1984). It appeared in two places in Poland around 1850 – botanical garden in Kwidzyn (German: *Marienwerder*) and Dłużyna (*Marianaue*) near Gryfino (Klinggraeff 1880 after Trepl 1984) and in the vicinity of Kraków (Berdau 1859). It was observed for the first time in Prague, the Czech Republic in 1872, the same year as it was observed in France. The other dates of its introduction are as follows: Belgium (1868); Austria (1870), the Netherlands (1885), Sweden (1870) and the Ukraine (1868) (Hegi 1965; Trepl 1984; Hultén, Fries 1986). It is not clear when the species arrived into the territory of Great Britain as two dates are given – 1848 and 1851 (Coombe 1956; Williamson 1996). The remaining part of the invasive range covers most of central Europe, France and the UK, with scattered localities in Scandinavia, the Baltic states of Latvia (1904) and Lithuania (1934) (Gudžinskas 1998; Hylander 1971; Hultén, Fries 1986; Verloove 2006) and in North America (Barkworth 1973). In North America the species is naturalised in northeast Canada, i.e., Quebec, New Brunswick, Nova Scotia and Prince Edward Island. At present it is observed in USA (EPPO 2011; Tanner 2008) but until recently it was not reported (Tabak, Wettberg 2008). As was mentioned earlier, the first habitats were botanical gardens and their close vicinity. In the next stages of invasion, the habitats that were invaded were predominantly gardens, parks and other sites in settlements (Trepl 1984; Tanner 2008). By the second half of the 19th century the species had been naturalised mostly in the deciduous forests of the northern and central part of Europe. Small balsam invaded forest interiors and their edges in forests; the former were usually disturbed sites at the beginning of invasion. Later in the 1900s, it became more and more able to penetrate into less disturbed and more natural forest habitats (Trepl 1984).

Dynamics and means of spread

Since its first introduction, the pace of the spread of *I. parviflora* has become much faster. For instance, its massive expansion in Poland started in the 1960s and now the species is very common on the territory of the country (Tokarska-Guzik 2005a). Small balsam is the third most common neophyte that is naturalised in the semi-natural vegetation in Germany (Kühn *et al.* 2004). The rate of increase of its range in Europe is unknown except for a few countries, e.g., the maximum rate of spread in the UK was calculated as 24 km per year in 1915 (Williamson 1996). Many authors stress that at the beginning of invasion, *I. parviflora* occupied only human-made or disturbed habitats such as botanical gardens, parks, cemeteries and roadsides (Trepl 1984; Csiszar, Bartha 2008; Obidziński, Symonides 2000). It appears that the species underwent the process of a lag-phase, which resulted in its faster spread and its entering into natural communities in the second half of the 20th century (Trepl 1984; Obidziński, Symonides 2000). During this time, the species changed its status from an epecophyte to (holo)agriophyte according to classification of synanthropic plants. It is not certain precisely when this happened. On the one hand, an extensive phytosociological survey in Westfalia (Wittig 1977 after Csiszar, Bartha 2008) showed that presence of *I. parviflora* was recorded in four of 800 relevés. On the other hand, a year later Ćwikliński (1978) presented the contribution of small balsam in natural forest communities including, among others, a floodplain forest, *Circaeo-Alnetum*; an oak hornbeam forest, *Stellario-Carpinetum* and a beechwood forest, *Melico-Fagetum*, *Fago-Quercetum*.

Autochorous dispersal mechanisms are not enough for the quick spread because seeds can only reach distances of up to 3.4 m (Trepl 1984). Kamieński (1884) after Tokarska-Guzik (2005a) claimed that the species was introduced accidentally by travelers who had arrived from Western Europe mainly by the sea. The transport of floating seeds by water is possible but probably of limited importance, although transport in river sediments with fast-moving waters in winter floods may contribute to long-distance dispersal (Tanner 2008). The majority of researchers agree that humans aided in the transport of the seeds of *I. parviflora*. Long distance forest management and the transport of timber played the most significant role. The occurrence of *I. parviflora* in various timber-yards in local parks and forests can be attributed to this pathway of migration. The frequent occurrence of *I. parviflora* along railways and tracks where trains that transported timber also supports this theory (Trepl 1984).

Single reports indicated that seeds might have been introduced along with buckwheat for peasants (Coombe 1956) or with soil and in the roots of garden plants, with flower seeds and

with compost as well. Epizoochorous dispersal in the fur of mammals and in the dirt on their feet was also reported as an important mode of long-distance dispersal (Trepl 1984). Graae (2002), in her experiment with domestic dog in a forest, found that despite the smooth surface of small balsam's seeds, dispersal on the backs of animals is possible. It was proved that roe deer and wild boar can transport the seeds of the plant (Heinken, Raudnitschka 2002). Another possibility for spread is the creation of microhabitats that are suitable for the germination of seeds. For instance, Piskorz, Klimko (2001) reported that soil that is rooted by wild boars (*Sus scrofa*) is also intensively colonised by *I. parviflora*, especially in strongly shaded sites that were previously covered with a thick layer of leaf litter. However, these are short-term changes that are closely related to repeated disturbances by animals. As Obidziński and Głogowski (2005) and Obidziński, Kiełtyk (2006) proved, zoopression, which is best exemplified by the red fox (*Vulpes vulpes*) and the Eurasian badger (*Meles meles*), may promote the spread of some species including therophytes. *I. parviflora* did not occur in the regions and forests that they studied – the Rogów District in central Poland and the center of Bialowieza Primeval Forest, respectively. However, it can be assumed that these animals could also facilitate the spread of small balsam.

Birds also transport seeds, which is manifested by the occurrence of *I. parviflora* in hollows or in crevices in the bark of living trees. Trepl (1984) reported that the dirt on the vehicles that a reused by foresters may contain up to 22 seeds per one litre of soil that is trapped in the tyres and other parts of a vehicle. Although some sources claim that the entire European population is derived from a single introduction in 1830 (Coombe 1956) such a fast spread contradicts this theory. According to Trepl (1984), individuals were brought into gardens out of botanical curiosity and were also sown into near-natural vegetation with the aim of "enriching" the natural flora (Trepl 1984, Tanner 2008). This method of propagation both in case of *Impatiens parviflora* and other plants is no longer used.

1.2.2. Impact on native biodiversity and the nature conservancy viewpoint

Opinions about the possible impact of *I. parviflora* on native and resident herbaceous flora are diverse. Hegi (1965) stated that the species in near natural forests can displace its native congener, *I. noli-tangere*. Later Sukopp (1962) disagreed because of the different biotopic requirements of the species. Trepl's (1984) observations showed that *I. noli-tangere* is substituted by small balsam only at suboptimal, bit drier habitats and in an optimal position; in moist habitats it retains its area and dominance. According to Faliński (1968; 1998a,b) and Kujawa-Pawlaczyk (1991), small balsam represents a substitutive relationship under

conditions of high light-availability and *I. noli-tangere* could possibly be replaced but this was a rather theoretical assumption. To date, none of the previous studies have indicated the negative impact of *I. parviflora* that resulted in the complete displacement of native species (Schmitz 1998; Obidziński, Symonides 2000; Kowarik 2003; Tanner 2008; Hejda 2012). When *I. parviflora* begins to penetrate into the herb layer sometimes, it can lead to the dominance of this species. This depends on the composition of the previous species and the availability of empty niches. The cover of bare ground and the low species diversity of resident plants seem to facilitate of the invasion of small balsam. Kujawa-Pawlaczyk (1991) believes that *I. parviflora* is an indicator of the degeneration of forest communities rather than a factor that causes it. The same problem was analysed by MacDougall and Turkington (2005) but in the case of alien invasive plants in general. They posed the question of whether alien plants benefit from disturbances or are the cause of disturbances in an ecosystem. Some studies (e.g., Łysik 2008) demonstrated an increase in *I. parviflora* cover and simultaneously a decrease of the cover of native species but any possible competitive ability of small balsam was not proven. Such changes that result in species poverty and disturbances or loss of ecosystem function can be a consequence of increasing human pressure rather than the influence of invasive alien species.

By analysing insects that feed on *I. parviflora* and aphidophagous insects that are associated with *Impatientinum asiaticum*, Schmitz (1998) drew the conclusion that the species supports biodiversity by enhancing rich fauna. Stary and Laska (1999) already formulated a similar opinion but only in relation to syrphid flies, especially in cultivated landscapes because small balsam plays a seasonal role as a food resource for them. Kujawa-Pawlaczyk (1991) and Faliński (1998b) claim that in deep forests with low light availability, *I. parviflora* is suppletive component of the herbaceous layer and this leads to an increase in the local biodiversity in natural plant communities. To date, no effect of the species and its distribution and abundance on the soil fauna and microorganisms has been observed (Csiszar, Bartha 2008).

1.2.3. Methods of control

In 1942 during World War 2, *Impatiens parviflora* was referred to as a "Bolshevik Mongolian invader" by the Nazis. The Reich Central Office of Vegetation Mapping, which was headed by the well-known phytosociologist, Reinhold Tüxen, demanded a "war of extermination" against small balsam in the areas that were supposed to belong to the homeland of Germany, i.e., the occupied areas of Poland (Barbour 1996; Simberloff 2003). In

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spite of such declarations, no attempts to remove this species were implemented. Only a few experiments to control *I. parviflora* (Csontos 1986; Adamowski, Keczyński 1998, 1999) have been published in literature. Both mentioned experiments that consisted of the removal of individuals by hand. In the previously mentioned study, 86% efficiency was noted and the abundance of the population decreased considerably. The author attributed the survival of *I. parviflora* in the locality that was studied to the seed bank of the species. The possible input of seeds from and adjacent area was excluded due to method that was applied. In the latter study, the authors described a successful attempt to stop an invasion of *I. parviflora*, although they emphasised that the treatment and monitoring should be repeated every year. Coombe (1956) indicated that cutting and pulling up the plants in their flowering phase before seed-set might be an effective control method due to the fact that the seeds germinate early in the spring. These kinds of methods are time and labour-consuming and thus they are only applicable at the initial stage of an invasion and in small areas. The control of populations of *I. parviflora* across a larger area or an entire country is not possible. Control activities can yield results only on a local scale and are desirable primarily in protected areas (nature reserves, national parks etc). A relatively efficient way to reduce the spread of small balsam and to reduce the size of the existing population in these areas is the elimination of ruderal habitats. Existing populations should be eliminated mechanically by pulling, digging or mowing. If the treatment takes place at the time of fruiting, plants that are removed should be burnt on the spot, thus reducing the risk of the further spread of the seeds (Solarz *et al*. 2005). Csiszar and Bartha (2008) reported that in some afforested sites that were overgrown by *I. parviflora* using herbicides successfully hindered germination, although herbicides such as glyphosate (commonly called roundup) cannot be used everywhere and e.g., in river valleys its usage is limited and it cannot be used at all times. Godefroid *et al*. (2007) showed that a recovery of *I. parviflora* was noted during tillage treatments. It turned out that from among several mechanical methods and pesticides, disc ploughing and glyphosate promoted the development of this plant. It should be noted that *I. parviflora* was not target species for application of methods of control in that study.

Biological agents could be another possible method of control. As was mentioned earlier, 13 phytophagous insects, at least two snails and five phytopathogenic fungi have been found on *I. parviflora*. Among them, *Puccinia komarovii*, which could kill whole population seems to be the most effective.

1.2.4. Economic importance

Small balsam, *I. parviflora*, is an alternative host for the black bean aphid, *Aphis fabae*, (Schmitz 1998), which is a major pest of sugar beet, bean and celery crops where a massive occurrence of aphids can cause the stunting of the plants. It is also a host for the cucumber mosaic virus CMV (Polak 1967; Brcak, 1979), which can attack many crop plants, apart from cucumbers, such as tomatoes, carrots, celery, lettuce, spinach and beets. It is well-known that CMV has a very wide host range (Zitter, Murphy 2009), so the possible role of *I. parviflora* in the spread of CMV is probably minimal.

Some reports have indicated that *I. parviflora* is possibly an edible plant. Griebel (1948) wrote that the leaves of small balsam contain a lot of vitamin C and when eaten raw could be source of this substance. This cannot be said about the shoots, which, if eaten raw can cause nausea. In addition, they contain a lot of oxalates and thus they are not recommended for people who are prone to kidney stones or arthritis, although the seeds have a pleasant nutty flavor and can even be eaten raw (Łuczaj 2002). Düll and Kutzelnigg (1988) after Tanner (2008) reported that the dried stems of the plants have been a source of food for people during times of famine. Like many other plants, small balsam can be used as a medicinal plant. Hydro-alcoholic extracts of the fruit and herbs made from the fruits are the most useful. Therapeutic treatments using extracts of *Impatiens* spp, including *I. parviflora*, are broad. The extract can be used as an anti-inflammatory, a diuretic, an antispasmodic, and an anti-psoriasis treatment. It inhibits autoimmunity immune and can be used against lupus, against atopic dermatitis, as an anti-acne treatment, an anti-androgenic treatment, a hypoglycemic treatment, an anti-atherosclerotic treatment, an anti-bacterial treatment, an anti-fungal treatment (systemic), an anti-allergic treatment. It works also as a mild laxative, protective liver, kidney and heart treatment. Preparations of balsam also prevent the hypertrophy of the prostate, kidney and urinary disorders of micturition (Różański 2009).

2. Methods

2.1. Study areas

The studies were conducted in several regions located in southern Poland – the Silesian-Kraków Upland (Silesian Upland, the Jurassic Upland) (Fig. 1) and the Cieszyn Foothills region and on single sites in the Republic of Hungary.

The Silesian Upland is a physical-geographical region that covers an area of nearly 4000 km^2, which is located in the southern part of Poland 50°15′N, 19°0′E. The region is characterised by a differentiated relief and geological structure with its central part being built of Carboniferous formations. It has also been heavily affected by the coal mining industry. As a result of human interference, the plant and soil cover has been substantially altered (Kozyreva *et al.* 2004). The exploitation of mineral resources began at the beginning of the Middle Ages and intensified in second half of the 18th century due to changes in economic activity, technical-scientific progress and urbanisation. The average air temperature reaches about 8° C and the annual precipitation is estimated to be ca. 700-800 mm. The prevailing winds are from the western sector (SW, W, NW). Many of the depressions and land deformations in woodland areas are the result of previous coal mining activity. This has led to the humidification or the desiccation of large areas. Colliery waste heaps, ground pits and subsidence reservoirs are characteristic features of the Silesian landscape. According to phytosociological studies by Cabała (1990), there are 17 forest associations and 26 syntaxa of lower ranks. The most dominant forest communities are pinewoods, *Leucobryo-Pinetum* W.Mat. (1962) 1973, *Molinio-Pinetum* W.Mat. et J.Mat. 1973, *Calamagrostio villosae-Pinetum* Staszk. 1958, and alder-ash carrs, *Fraxino-Alnetum* W.Mat. 1952. Oak-hornbeam forests, *Tilio-Carpinetum* Tracz. 1962, along with beech woods, *Dentario-glandulosae-Fagetum* W.Mat. 1964 ex Guzikowa et Kornaś 1969 are less common. Floodplain forests, *Salici albo-fragilis* R.Tx. 1955, *Populetum albae* Br.-Bl. 1931, are the most weakly developed. One of the most dominant forest communities is *Querco roboris-Pinetum* (W.Mat. 1981) J.Mat. 1988 due to massive plantation of Scots pine, *Pinus sylvestris*, in the habitats of deciduous forests. Therefore, the origin of this type of vegetation is anthropogenic. The majority of primary forests were cleared and converted into arable lands or wastelands and - urbanised industrial areas. Some of these were afforested mainly by coniferous species and occasionally by deciduous species (Nyrek 1975). There are probably some remnants of ancient forests resulting from habitat continuity and quality but they have been exploited by foresters (Cabala 1990). Thus, the forests that exist in the area are rather recent forests.

The Jurassic Upland (Kraków-Częstochowa Upland) is located in Southern Poland and borders on the Silesian Upland. This region covers an area of about 2615 km^2 and is mostly built from Jurassic dolomites. The characteristic elements of the landscape are limestone rocks and numerous caves. The mean elevation of the area is about 350 m a.s.l. The soils of this area are rather poor; 60% are podzolic soils and brown soils occur more rarely. These most frequently occur in the Olkusz Upland. The river network is weakly developed due to the high permeability to precipitation of Jurassic lime. The biggest rivers are: the Przemsza, the Rudawa, the Prądnik, the Dłubnia and the Pilica. All of them supply the Wisla with water. The mean annual temperature is ca. 7.5°C and is lower for the whole country. The mean annual precipitation amounts to ca. 700 mm but it increases in a southward direction. The vegetation period lasts from 201 to 211 days and is also about two weeks shorter than in the adjacent areas except for a part of the upland in the east (Urbisz 2004).
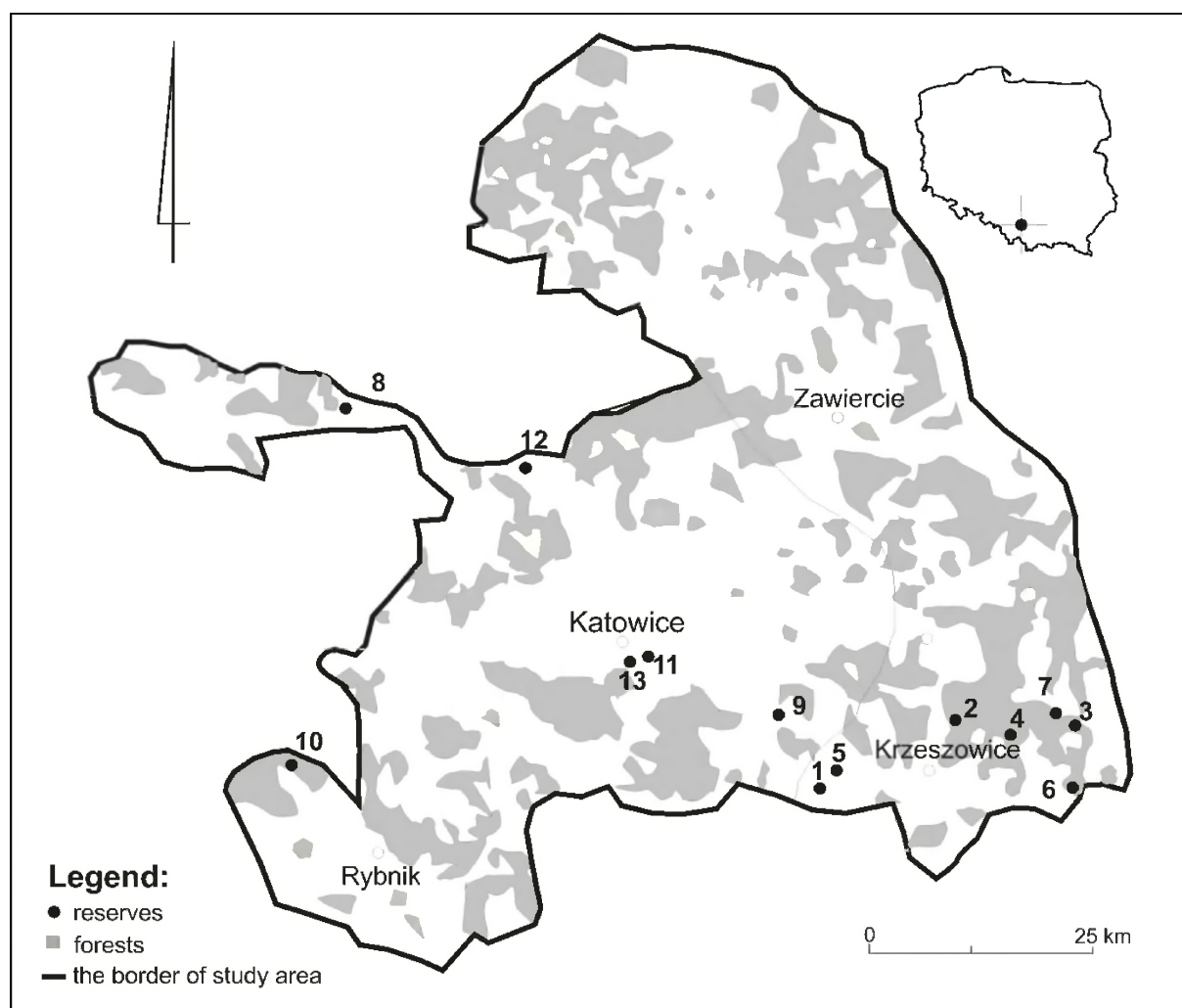
Fig. 1. Study area – The Silesian-Kraków Upland. Numbers indicate the nature reserves where the permanent study plots were established. For a description of the nature reserves see Table 4

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Impatiens parviflora is quite a frequent species in both areas. It is more common in the western-southern part of the Silesian Upland while the species grows more frequently in the southern part of the region in the Jurassic Upland (Fig. 2).
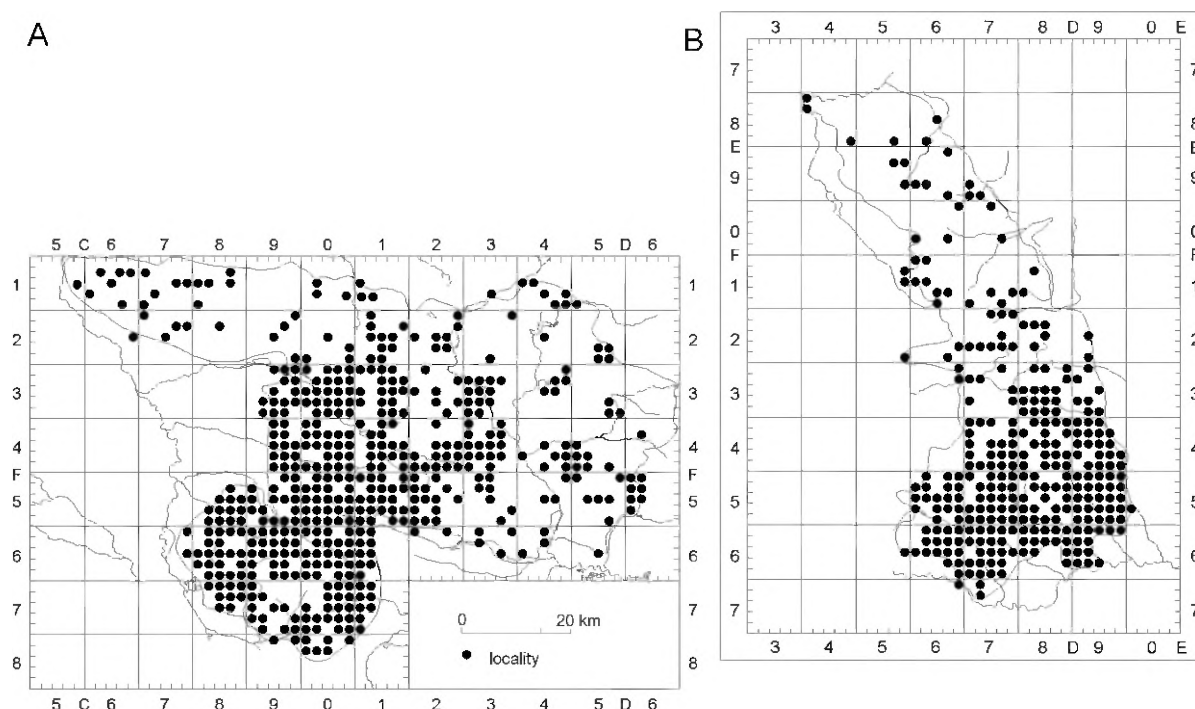
Fig. 2. Distribution of *Impatiens parviflora* in the study area (Chmura, Urbisz 2005). A – Silesian Upland, B – Jurrasic Upland

2.2. Habitat research

Soil samples were taken on the sites where the permanent plots were established and on randomly selected sites where the phytosociological relevés were performed.

Four soil sub-samples were collected from the topsoil from 0-20 cm depths and then mixed into one composite sample. Each sub-sample was taken from the rhizosphere of *Impatiens parviflora*. After air-drying and sieving over 2 mm, the samples were analysed for pH, measured potentiometrically in H_2O and in 1N KCl. Total organic C (%) was measured according to the Tiurin method. Loss on ignition was tested in a muffle furnace (%) and total N content - N_T (%) was determined using the Kjeldahl method. Available Mg was detected using FAAS (Flame Atomic Absorption Spectrometry), available phosphorus P in an ammonium lactate extraction was done using the colorimetry method, sodium Na and potassium K were detected using flame emission spectroscopy and Ca by spectrophotometry in 1 N ammonium acetate (mg/kg) (Lityński *et al*. 1976; Ostrowska *et al*. 1991). The content

of $CaCO_3$ was analysed using the Scheibler method. Granulometric composition was measured using the aerometric method and the sieve method. Fractions of mineral grains in sizes of between <0.0002 to 0.02 mm were classified as floatable parts. The results of the analyses are presented on figures in the form of ecodiagrams (Zarzycki 1976; Borysiak 1984; Szwed 1986) that show the percentage of the occurrence of *Impatiens parviflora* as distinguished by aspect, soil properties and litter depth and other soil variables. Soil reaction, i.e., pH in water and KCL solution are given after Piękoś-Mirkowa *et al.* (1996). In order to characterise the pH of soil, a modified scale according to Fotyma *et al.* (1987) after Piękoś-Mirkowa *et al.* (1996) (Tab. 1) was used. The scales of the available nutrient content of phosphorus, potassium, magnesium, organic carbon and total nitrogen were adopted after Piękoś-Mirkowa *et al.* (1996) and the literature cited there. The following classes were used: 0-10%, 10.1-20.0%, 20.1-30.0%, 30.1-40.0 and more than 40.0% in the diagrams that show the content of loss on ignition. The content of calcium was divided into six classes [mg/100g]: 0.0-200.0, 200.1-400.0, 400.1-600.0, 600.1-800.0, 800.1-1000.0, >1000.0. In addition, six classes were applied in the case of sodium [mg/100g]: 0.0-10.0, 10.1-20.0, 20.1-30.0, 30.1-40.0, 40.1-50.0, >50.0.

The 7-degree scale of the percentage of the floatable fraction and the division of soils into groups according to granulometric composition were employed according to Kuźnicki *et al.* (1979). The 5-degree scale of litter depth was used after Obmiński (1977).

Tab. 1. Scale of soil reaction

Reaction	pH	
	in H_2O	in KCL
Very strongly acid	<4.1	<3.5
Strongly acid	4.1- 5.0	3.5 - 4.5
Acid	5.1- 6.0	4.6 - 5.5
Slightly acid	6.1- 6.7	5.6 - 6.5
Neutral	6.8 -7.4	6.6 - 7.2
Alkaline	>7.4	>7.2

In the diagrams showing the C:N ratio, the scale of humus was adopted after Duchaufour (1970) after Piękoś-Mirkowa *et al.* (1996). According to these authors, the C:N ratio estimated at ca. 10 demonstrates humus of a calcimorphic type. A forest of a mull type is indicated by C:N < 20 and it most frequently ranges from 12 to 15. The range for moder is 15-25, while for mor it varies from 30 to 40. Thus, the intervals were established as follows: C:N: <10.0, 10.1-15.0, 15.1-20.0, 20.1-25.0, >25.0.

The scale of the content of the elements (P, K, Mg) that was available to plants was adopted after Piękoś-Mirkowa *et al.* (1996) (Tab. 2). A Lutron LX-105 light-meter was used to characterise the light conditions under the tree canopy layer. Five records were taken within the plot. The light quantity was expressed as a percentage of the light conditions as measured in an open area nearby at the same time. The canopy-scope was used as an alternative method of canopy openness measurement (Brown *et al.* 2000; Salachna, Chmura 2013).

Tab. 2. The scale of contents of nutrients

Content	P_2O_5	K_2O	MgO
Low	<3	<7	<10
Middle	3.- 9	7. - 14.	10. - 20.
High	9.- 18.	14. - 28.	20. - 40.
Very high	>18	>28	<40

The Spearman rank correlation test was used to test relationships between the cover-abundance of *I. parviflora* and selected soil parameters.

In addition to the direct field measurements, the Ellenberg indicator values system, EIVs, were used. The indicator values for light (L), continentality (K), temperature (T), moisture (F), reaction (R) and nitrogen (N) were taken from Ellenberg *et al.* (1992). The mean arithmetic EIVs were computed on the basis of the presence/absence of the species in herb layer. They were assigned as: mL, mR, mK, mT, mF and mN, respectively. The species that were assigned x, i.e., considered to be indifferent were omitted from the calculations. *Impatiens parviflora* was also excluded from the calculations. In order to assess whether the invaded sites could be studied using phytoindication methods, the Spearman rank correlation coefficients between environmental variables (soil parameters) and the mean indicator values were calculated.

2.3. Population studies

In order to study variations in the seed mass of *Impatiens parviflora*, seed samples were collected in two countries, Poland and Hungary, in 2010 in natural and semi-natural forest communities (Csontos *et al.* 2012; Chmura *et al.* 2013) and they were collected in Poland once again in 2011 and 2012. They were collected at the full-ripe stage. The seeds were kept in paper bags under the same room temperature conditions until the date of the measurements. During storage, the weight of the seeds was monitored until it was stable at

which time five 50-seed lots were formed from each sample and measured using an analytical balance with 0.0001 g accuracy. The viability of seeds was tested using the so-called "apparent viability" method (Zelenchuk 1961; Csontos *et al.* 2012, Chmura *et al.* 2013). The mass of the 50-seed lots between sites was analysed using the analysis of variance ANOVA test and the LSD Fisher test for multiple comparisons.

Different regimes were applied to study the conditions of germination. In total there were 60 samples of seeds (100 seeds in each). Seeds were kept air-dry in paper bags. During stratification they were wet and kept in the dark. The effect of stratification temperature, storage temperature and time of stratification as well as habitat were analysed. Seeds were germinated in Petri dishes at 5° C in the dark.

Tab. 3. Basic parameters of the study sites where the seed samples of *Impatiens parviflora* were collected. H1-4 samples were collected in Hungary; P1-7 samples were collected in Poland (Csontos *et al.* 2012; Chmura *et al.* 2013 and author's own studies)

Code	Locality	Latitude N	Longitude E	Date
H1	Vadálló rocks,Visegrádi Mts, Hungary, karst forest	47°44'22"	18°54'50"	24.08.2010
H2	Rumi forest at the Rába River, Hungary	47°06'41"	16°50'45"	02.09.2010
H3	Kis-Sváb Hill, Budai Mts, thickets	47°30'12"	19°00'47"	22.07.2010
H4	Near the village of Rábahídvég; along an earth-covered road in a Floodplain forest (mainly formed by willow, poplar and ash) on the bank of the Rába River	47°03'54"	16°44'59"	31.08.2010
P1	Katowice, Poland, managed forest with *P. sylvestris*	50°12'8.31"	18°57'26.13"	04.08.2011
P2	"Bukowica" nature reserve near Wygiełzów, *Dentario glandulosae Fagetum*	50°4'45.81"	19°24'59.48"	18.09.2011
P3	Soblówka near Ujsoły, Beskid Żywiecki Mts., Poland	49°26'13.6"	19°08'33.7"	20.09.2011
P4	"Skala Kmity" nature reserve, Zabierzów near Kraków, Poland	50°06'13.24"	19° 49'8.06"	18.09.2011
P5	Jasieniczanka, Bielsko-Biała	49°52'53.34"	18°57'16.45"	22.09.2011
P6	Village of Cisownica near Ustroń, *Tilio-Carpinetum*	49°42'57.43"	18°45'52.26"	23.09.2012
P7	Katowice, along a forest path, mixed deciduous forest along the Mleczna River	50°12'8.3"	18°57'26"	23.09.2012

Differences in the germination percentage due to the types of habitats (oak-hornbeam forest, *Tilio-Carpinetum*; alder forest, *Fraxino-Alnetum* and forest path (seeds were gathered in the vicinity of the two forest communities mentioned), stratification temperature (3.5° C vs -2.5° C), storage temperature (8.5° C vs 20° C, only for 3.5° C and 2.5° C of stratification temperature and all habitats combined), time of stratification (for all of the remaining habitats and treatments combined) were analysed using G – tests.

Morphological variation

In order to characterize the morphological variation of *Impatiens parviflora* among various forest types 415 individuals in total were selected for morphometric studies. The individuals were selected from forest interiors under the tree canopy in deep or moderate shading conditions. Sites were situated in patches of the four forest communities that are found most frequently in the Jurassic Upland – *Dentario glanduloase-Fagetum, Tilio-Carpinetum, Fraxino-Alnetum and Querco-roboris-Pinetum*. These four plant communities are quite common in the nature reserves in this region. As was pointed out by Szary and Michalik (1998) using the example of the Dolina Racławki nature reserve, the topographic diversity of the vegetation that covers the hills shows a similar pattern. At the bottom of the hills, usually in the river valleys, there are habitats of the *Ulmenion* alliance communities, while patches of oak-hornbeam forests (*Tilio-Carpinetum*) are situated in the higher areas and finally close to top and on the top of the hills, there are phytocoenoses of beechwoods (*Dentario glandulosae-Fagetum*, *Luzulo-pilosae-Fagetum* and on the southern slopes *Carici-Fagetum* or mixed coniferous forests. Ten randomly chosen individuals were subjected to measurements on the site. The following variables were measured: the height of plant, the width and length of leaves and the number of flowers and fruits per plant. The height of plant was defined as the distance from the ground level up to the top of a shoot. The length of a leaf was determined for the longest leaf of a plant. The width of a leaf was determined as the widest area of the longest leaf. The number of flowers included all of the flowers that were counted per a plant as was the number of fruits.

Variations in the above-mentioned plant traits are shown on histograms with a fit to the normal distribution. The Spearman rank correlation test was used to determine whether the soil parameters had an influence on the plant traits that were chosen or whether there was a correlation between the morphological plasticity and environmental variables. The Kruskal-Wallis test and Conover test for pair-wise comparisons were used to determine the significance of any differences in particular plant traits between the distinguished forest

communities. Principal Component Analysis (PCA) was used to reduce the dimensionality and to select the most explanatory variables based on the value of the eigenvalues.

Phenology

Based the Piskorz and Klimko (2002), the following phenophases in *I. parviflora* were distinguished: 1 the two-cotyledon phase, 2 the one-cotyledon phase, 3 the vegetative phase (stems without flower buds), 4 the preflowering phase (flower buds present), 5 the flowering phase (open flowers present), 6 the prefruiting phase (with unripe fruits), 7 the fruiting phase (with ripe fruits), 8 the subsenile phase (with declined leaves), 9 the senile phase (stems without leaves). The frequency of the particular phenophases between the four forest communities, *Dentario glanduloase Fagetum, Tilio-Carpinetum, Fraxino-Alnetum, Querco roboris-Pinetum* and at forest margins of the above-mentioned forest types over the vegetation season from 16.04.2007 to 30.09.2007 in a 12-time series was observed. From 57 to 80 marked individuals in each type of habitat were studied in terms of the number of cotyledons, flower buds and flowers and unripe and ripe fruits.

The participation of the phenophases in particular forest types was analysed using contingency tables that were designed to find any significant differences between them. The frequencies between the time series and the distinguished forest type were checked using the G-test for each phenophase. Only those time series for which at least one individual representing a given phenophase in at least one forest type were taken into account.

Spatial and temporal variation in life history

The morphological variation of *I. parviflora* among microhabitats was analysed in one forest community, *Dentario glandulosae Fagetum*, in the area of the "Bukowica" nature reserve. Microhabitats within the forest environment were chosen based on the study by Klama (2002) with the author's modifications. Klama (2002) distinguished 30 types of microhabitats, which he referred as "substrates" or "terrain microforms". Of the list of microhabitats, only those were chosen that were available in the study area (in at least five replicates) and that were occupied by *I. parviflora*. The situation of the chosen microhabitats is shown on Figure 3. Only one type represented an anthropogenic one – a forest path that was created because of forest management. The others are natural forest types of habitats that can be encountered in deciduous forests and that are associated with natural disturbances such as wind tree falls or forest self-thinning processes.

The list of microhabitats includes: Forest interior – soil under tree canopy (1); Canopy opening – soil under the canopy opening (2); Area near a log – area near a lying decaying dead log (3); Log under canopy – bark on a decaying dead log of *Fagus sylvatica* from 1st to 7th of 8 classes of dead wood decomposition according to the classification by Holeksa (2001) (4); Log under the canopy opening – bark on a decaying dead log under the canopy opening (5); Root plate – soil in the root plate of dead logs (6); Tree fall disturbance – holes in the ground after a tree has fallen (7); Hollow – tree hollow in a living tree (8); Path – soil on a forest path (9), Root collar – base of a living tree (10); Stump – decaying top of stump (11) (Fig 3.). For sites situated on soil, i.e., forest interiors, random 1 m^2 squares of the canopy openings and forest paths were established. For other types of microhabitats, the selected area depended on the particular objects.

Only ten individuals were randomly chosen on each site for morphometric studies because the populations of *I. parviflora* were small on some sites.
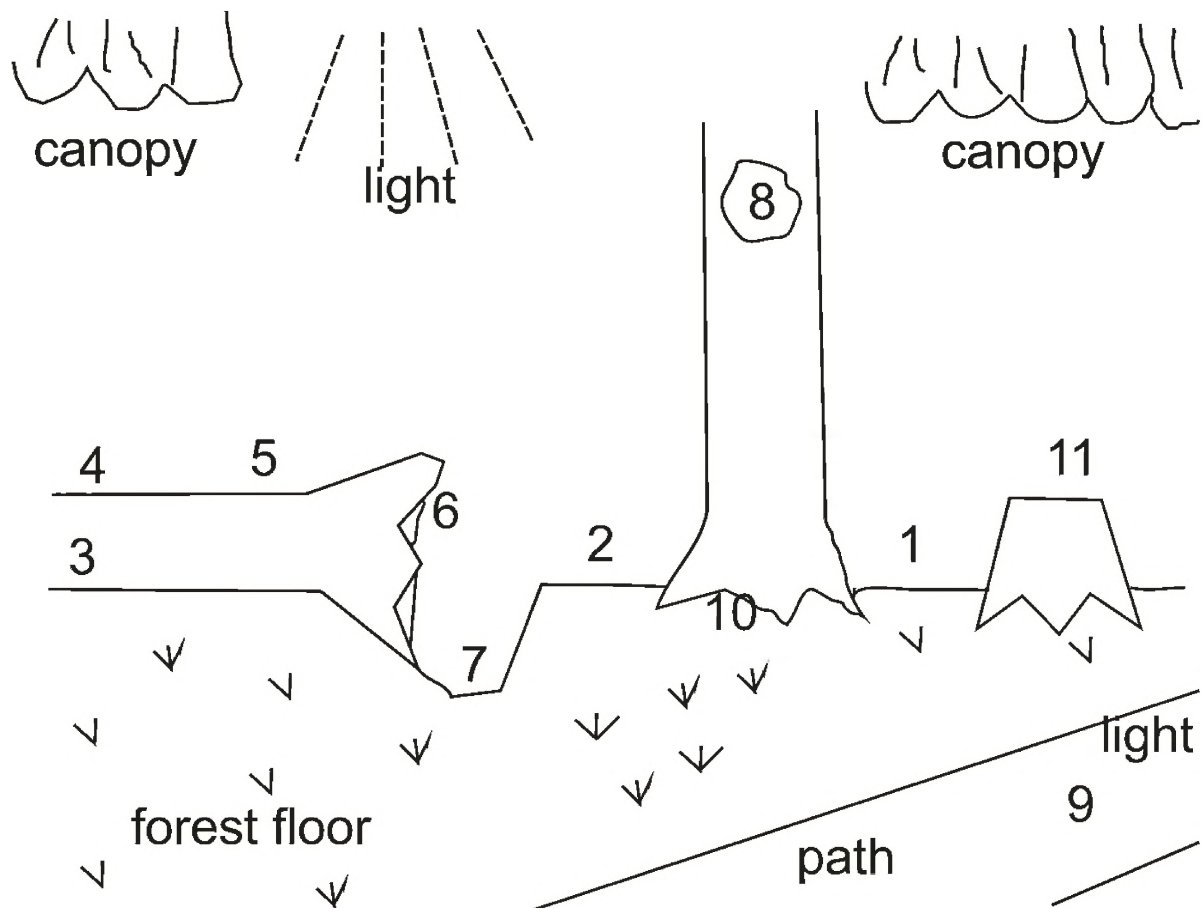

Fig 3. The scheme that shows the types of microhabitats that can occur in a forest. Explanations: 1: canopy; 2: canopy opening; 3: area near a log; 4: log under the canopy; 5: log under the canopy opening; 6: root plate; 7: tree fall disturbance; 8: hollow; 9: path; 10: root collar; 11: stump

The following parameters were considered – the height of the stem; the number of flower buds; the number of flowers; the number of fruits and the presence of cotyledons [%]. The measurements were conducted in mid-June 2006.

Because of the high degree of variations in the habitat conditions within the selected microhabitats, the light conditions were measured using a Lutron LX-105 light meter. In addition to light availability, selected edaphic conditions were also analysed, i.e., C:N, the content of Ca, $CaCO_3$, loss on ignition, Mg, Na, P and K. In order to estimate the edaphic conditions, soil samples or samples of the substrate (decaying bark with initial humus; remnants of soil at the root plate of fallen trees in the case of a dead wood complex), were collected if they were available. The substrate material was sieved and underwent the procedures that were described in Chapter 2.2 Habitat Research. In addition to the environmental variables for each site, the cover of all of the vascular plants were estimated visually using 1,2,5,10…100% intervals. The entire area of the distinguished types of microhabitats was taken into account with the exception of forest interiors, canopy openings and forest paths. A similar procedure was applied by Zielonka and Piątek (2004) for the rotten logs of spruce, *Picea abies*.

At least 10 randomly and marked plants were observed from 16.04.2007 to 22.09.2007 for the temporal study of variations in the life-history traits among the distinguished microhabitats. Seedling survival (%) was counted and seedling height, the number of leaves, the number of flower buds, the number of flowers as well as the number of fruits was assessed during the vegetation season in a six-time series.

In order to examine any differences between microhabitats in the spatial study of variations in the life history traits, the Kruskal-Wallis test was used followed by a post-hoc Conover test. G-statistics were computed to test any differences in the percentage of cotyledons between microhabitats. PCA was used to analyse which traits were the most explanatory. Redundancy Analysis (RDA) was used to assess the impact of environmental variables that were measured and the number of accompanying species on the traits of *I. parviflora*. The Monte Carlo test with 499 permutations was used to calculate the first type of error – p.

The Kruskal-Wallis and Conover tests were also used to assess the significance of any differences in the mean variables of the life history traits between microhabitats over the time in a six-time series.

Influence of the presence of dead wood and light on the behaviour of the species.

In order to estimate the impact of light availability (canopy openings) and the trophy of a forest habitat due to the enrichment of soils by nutrients from dead wood decomposition, 152 individuals were measured in four types of habitats: C – canopy (control habitat: soil under a canopy of trees, CW – canopy and dead wood (neighbourhood of decaying dead logs under a tree canopy), O – openings (soil under canopy openings) OW – openings and dead wood present (neighbourhood of decaying dead logs under canopy openings). In order to avoid pseudoreplication *sensu* Hurlbert (1984) and a high variation in the measurements of the distinguished habitats, the plant harvests were conducted at the same time but from many sites and were repeated in two succesive years (2007-2008) beginning in 2006. The following plant traits were analysed: plant height (cm), the size of the longest leaf area, LA, (leaf area cm^2); the biomass of a leaf, LB, [g] and the ratio of the leaf area to the dry biomass of a leaf, SLA, (specific leaf area). The leaves were dried for 48 hours at a temperature of 60° C. Two-way ANOVA was used to test the impact of light availability in the canopy openings and the presence of dead wood on the size of plants and leaf traits. The Student test with the Bonferroni-Holm correction was adopted for multiple comparisons (Holm 1979).

2.4. Phytosociological research

A modified Braun-Blanquet method with 0,1,2,5,10,20…100 % intervals was applied for the estimation of species abundance in the phytosociological records (10 m x 10 m). Using the random-stratified method (Dobosz 2004; Godefroid *et al.* 2005; Chmura 2013, 2014), 485 relevés were taken in 52 forest complexes (Fig. 1) in the Silesian Upland. The relevés were distributed according to a pre-established framework on the basis of forest stands, pedological (Strzemski and Witek 1978), topographical and geological (Kondracki 1998) and a potential vegetation map (Matuszkiewicz 2008) for the stratified sampling. In order to avoid the risk of omitting smaller topographic units, i.e., parts of the region that differed in relief, soils and land use, the types of forests sites for the relevés were distributed within the entire area of the Silesian Upland. The relevés were only taken in forest interiors. Crop plants sites and those sites that were places of a disturbance such as the vicinity of forest paths, roads and cutting areas were excluded from the study. All relevés were done in the patches where invasive alien plant species can be encountered in this area (Chmura 2004). The invasive alien species were supposed to be in the phase of naturalization in the patches of vegetation, i.e., the presence of seedling or juvenile individuals in herb layer in the case of woody plants.

The collected material was stored in a table using JUICE 6.3 software (Tichý 2002).

The phytosociological affiliations of species were adopted after Matuszkiewicz (2008), the names of plants after Mirek *et al.* (2002) (also available online: http://info.botany.pl/czek/check.htm).

Based on the obtained cover data in order to estimate the degree of the naturalisation of an invasive species, the percentage cover of neophytes in relevés was calculated according to the following formula (Chmura, Sierka 2006b):

$$D_N = \frac{\sum C_{NI}}{\sum C_{ALL}} \times 100\%$$

where: D_N = the degree of neophytisation (*sensu* Olaczek 1974, see also Łaska 2001), C_{NI} – the sum of the cover of all neophytes in the relevé, C_{ALL} – the sum of the cover of all of the species in the relevé.

In order to estimate the role of a particular neophyte in the neophytisation of a community, its percentage of relative cover P_N was computed according to the following formula:

$$P_N = \frac{C_N}{\sum C_{NI}} \times 100\%$$

where: P_N = participation in the neophytisation, C_N – the cover of neophyte in relevé, C_{NI} – the sum of cover of all of the neophytes in the relevé.

In order to test which syntaxonomical groups of species *I. parviflora* is accompanied by, the Spearman rank correlation was used to analyse the relationships between the cover of *I. parviflora* and the total cover of representatives of particular phytosociological classes – *Querco-Fagetea, Vacccinio-Piceetea, Alnetea glutinosae* and *Quercetea robori-petraeae.*

2.5. Studies on permanent plots and long-term research

In the years 2004-2012 fourteen nature reserves in total were subjected to phytosociological and population studies (Tab. 4). A total of 68 permanent study plots were laid out including 38 in the Silesian Upland and 30 ones in the Jurassic Upland in 2004. Ten permanent study plots were established in six nature reserves of the second region for long-term research (LTR) between 2005 and 2012. The 3-year research was conducted on one permanent study plot in the Ochojec nature reserve during the period of 2005-2007 (Sierka *et al.* 2009).

The size of study plots covered an area 100m². They were laid out in various forest communities including riparian forests, oak-hornbeam forests, beech woods and mixed coniferous forests. Each study plot was divided into 100 subplots of 1 m² (Chmura, Sierka 2006a). The species composition of field layer was noted on each subplot. The cover of plants was estimated visually using the following scale: 0,1,2,5,10,20...100 %. The total cover of all of the plants that were present could exceed 100%.

The biodiversity indices were calculated for all of the subplots:

Shannon-Wiener index:

$$\textbf{\textit{H}}\textbf{'} = -\sum p_j \ln p_j$$

where: pj is the contribution of a species (percent cover) of the j-th species.

Shannon's evenness index (= Pielou's evenness index=J' H/H max):

$$\textbf{\textit{E}} = H/H_{max}$$

where H is the value of the Shannon-Wiener index and H max is the H value when all of the species in a sample have an equal contribution. The greater the value of the index, the more equal the abundances of the species that were present in a sample.

Simpson's diversity index:

$$\textbf{\textit{D}} = 1/\sum_{i=1}^{S}(p_i^{2})$$

The value of this index ranged between 0 and 1; the greater the value, the greater the sample diversity. In this case, the index represented the probability that two individuals that had been randomly selected from a sample would belong to different species.

S was also determined for each study plot as a measure of species richness.

The species from the study plots were classified into several plant functional types according to the concept of Semenova and Van der Maarel (2000). Among others, species were classified by their life form according to Raunkiaer, given after Zarzycki *et al.* (2002) and by their dispersal mode following the classification of Kornaś (1972) (i.e., autochore, barochore, endozoochore, epizoochore, myrmecochore and hydrochore). Affinities of a species to a particular plant functional type were taken from several sources – Kornaś (1972), Dzwonko and Loster (2001), Frank and Klotz (1990) and Jacquemyn *et al.* (2001). Ecological strategies according to Grime (1979) were adopted after several sources – Frank and Klotz (1990) and Dzwonko and Loster (2001). Seven strategy types were used – three fundamental ones, i.e., competitor (C), stress tolerater (S) and ruderal (R) and four intermediate strategies that are

indicated by the corresponding letters (CR, CS, SR, CSR). Further intermediate types were pooled as suggested by Hermy *et al.* (1999).

Tab. 4. The list of the nature reserves situated in the Silesian-Krakow Upland (Jurassic Upland - KC and Silesian Upland - SU) that were studied. The number of study plots are given for studies in the years 2005-2012, *-2005-2007

Name of reserve	Area ha	Latitude	Longitude	Region	Number of permanent study plots for long-term research
1. Bukowica	22.7	50°04'43"N	19°23'55"E	KC	2
2. Dolina Eliaszówki	109.57	50°10'18"N	19°38'02"E	KC	2
3. Dolina Kluczwody	35.22	50°09'54"N	19°49'10"E	KC	1
4. Dolina Racławki	473.9	50°09'49"N	19°41'33"E	KC	1
5. Lipowiec	12.44	50°04'42"N	19°26'38"E	KC	2
6. Skała Kmity	19.36	50°06'06"N	19°48'38"E	KC	2
7. Wąwóz Bolechowski	22.44	50°09'30"N	19°46'55"E	KC	
8. Hubert	13.47	50°32'42"N	18°26'49"E	SU	
9. Dolina Żabnika	42.33	50°13'03"N	19°23'53"E	SU	
10. Łężczok	396.21	50°08'01"N	18°16'27"E	SU	
11. Ochojec	25.73	50°12'24"N	19°00'07" E	SU	1*
12. Segiet	24.99	50°24'18"N	18°50'53"E	SU	
13. Las Murckowski	100.67	50°11'32"N	19°3'41"E	SU	

In order to study the effect of scale on the relations (Stohlgren *et al.* 2006) between *I. parviflora* and native species, differences in plant functional types were compared at several levels – the floristic level, a high scale and a low scale. The floristic level comprised the number of species belonging to the aforementioned groups, which were divided into two groups – those accompanying *I. parviflora* (species that occurred in subplots that were occupied by the species) and species that were present in the invaded subplots. The high scale, i.e., level of 100m^2 – total frequencies of species in the subplots that were either occupied or non-occupied by *I. parviflora* was taken into account. For the third level, the low scale of 1 m^2, the total cover of plant functional types were computed for subplots of 1 m^2. TriGraph software (Legg 2004a) was used to compare the Grime strategies at the floristic level and CSR Bubble Plot was done. The Mann-Whitney test was used to examine any differences between the two groups of species at the distinguished scale levels.

The Spearman rank correlation test was used to test the hypothesis that the number of species and the cover of resident species affect the cover of *I. parviflora* in relation to all 68 plots combined and for the plots in the Jurassic Upland and the Silesian Upland separately for 2005. The correlations were repeated in 2006 for the plots of the Kraków-Częstochowa

Upland. In addition, the density (the number of individuals of *I. parviflora*) was correlated with species richness and the cover of native plants in this region in 2005 and 2006.

The Mann-Whitney test (Wilcoxon sum rank test) was used to examine any differences in the number and cover of native species in the presence and absence of small balsam. This procedure was done separately for the study plots from the Jurassic Upland and the Silesian Upland.

For ten selected study plots (LTR plots), each of which is situated in the Jurassic Upland, the studies were continued. Sampling of herb layer vegetation was carried out in the peak of vegetation season (mid-June till mid-August). These study plots differed in the invasion level by *I. parviflora* at the beginning of the long-term research. For two first years, 2005 and 2006, within a five-metre belt of the border of the LTR plot, each individual of small balsam was removed in order to isolate the population from the plants in the vicinity. Any other new plants that appeared in the remaining years were regarded as individuals that had developed due to the self-dispersal of the population within the LTR plots.

The LTR plots can be divided into the three groups – 1) the <u>initial invasion group</u> – frequency not higher than ten. This group contained two study plots nos. 3 and 8 – the patch of *Dentario glandulosae-Fagetum* in the "Dolina Racławki" nature reserve and the patch of oak-hornbeam forest, *Tilio-Carpinetum*" with *Aconitum moldavicum*, in the "Skala Kmity" nature reserve, respectively. The next group 2) <u>intermediate and advanced invasion group</u> – contained five study plots with a frequency of 37-66 occupied subplots per study plot. These were study plots nos. 2, 10, 5, 9, 1 – two patches of *Tilio-Carpinetum* in the "Dolina Eliaszówki" nature reserve and one from the "Dolina Kluczwody" nature reserve and one site of beechwood, *Dentario glandulosae-Fagetum*, from the "Bukowica" nature reserve. The next one was the riparian forest, *Fraxino-Alnetum*, in "Skała Kmity". The last group 3) <u>saturation invasion group</u> encompasses three study plots, with a frequency at least 90 invaded subplots, nos. 4,6,7 – two patches of *Tilio-Carpinetum* from the "Lipowiec" nature reserve and the phytocoenosis of *Dentario glandulosae-Fagetum* in "Bukowica". In addition to recording the cover of each of the vascular plants in the subplots within the study plots, the spatial structure of the *Impatiens parviflora* population was determined following Chessel (1977) after Falińska (2004).

Additionally, in the LTR plots in 2005 and 2006 the cover of bare ground and ground that was exclusively covered by *I. parviflora*, the cover of litter and the total cover of gaps (other empty sites in the herb layer, including stones, mobile wood rests, trees – all substrates that were not occupied by a species) were estimated. The density of *I. parviflora*, i.e., the

number of shoots (individuals), was assessed in each subplot of the study plots. A 1m x 1m wooden frame was used to collect all of the data within the subplots for measurements in the field. In the remaining years only the cover of all species were noted and measuring tape was used instead of a wooden frame in order to minimise the effect of trampling on the ground flora and the dispersal of seeds by *I. parviflora*.

The Spearman rank correlation coefficients were calculated in order to test the relations between a disturbance in the herb layer (bare ground, ground covered by litter) and the density and cover of *I. parviflora*.

The contingency tables (G-test) were used to assess any differences in the frequency of *I. parviflora* between the years. Differences in the total cover over the years was checked using the Kruskal-Wallis test followed by a post-hoc Conover test, whereas the Friedman rank test followed by the Conover test were used between the years in the same occupied subplots.

The phenomenon of autocorrelation may occur in the afore-mentioned studies, especially when the variables that are computed based on vegetation data from the subplots were subjected to correlation tests. It is noteworthy that similar correlation tests, in which the data from subplots within transects, i.e., spatially autocorrelated sites, were performed by Obidziński and Symonides (2000). This phenomenon of autocorrelation accompanies almost all natural processes. It is the spatial relationship of the values of variables that results from the spatial continuity of the environment (Kapusta 2004 after Franiel 2012). This problem will always be present in cases in which the study plots are divided into smaller subplots. There is a high probability that adjacent study plots are similar in terms of habitat properties and species composition due to their close proximity. Thus, subplots cannot be regarded as independent samples as observations, but on the other hand, it was revealed that the study plots are rather heterogenic, which was manifested by the high beta-diversity (among the subplots within the study plots) (Chmura, Sierka 2006a). The correlation coefficients, which were computed based on the variables that were taken from subplots, showed a similar trend as the correlations between the variables from the independent samples (study plots), e.g., a negative significant correlation between the beta-diversity of the native flora and the frequency of *I. parviflora* in the study plots. Moreover, to reduce any possible autocorrelation, additional data sets, i.e., 1000 randomly 1 m^2 subplots with different abundances of *I. parviflora* in each of the two regions that were studied were analysed in terms of the cover of all of the species that were present and were also subjected to correlation analyses.

2.6. Mycorrhizal research and biotic studies

Studies on arbuscular mycorrhiza, AM

The methods in mycorrhizal studies were described in detail in the paper by Chmura and Gucwa-Przepióra (2012). A total of 900 one-cm long root pieces were taken from the topsoil of 30 sites in the Jurassic Upland and subjected to laboratory analyses according to the modified method by Phillips and Hayman (1970). The following parameters of arbuscular mycorrhisation (AM) were recorded: mycorrhizal frequency (*F%*) – the ratio between root fragments that had been colonised by AMF mycelium and the total number of root fragments that were analysed; relative mycorrhizal root length (*M%*) – an estimate of the amount of root cortex that was mycorrhizal relative to the whole root system; the intensity of the colonisation within individual mycorrhizal roots (*m%*); relative arbuscular richness (*A%*) – arbuscule richness in the whole root system and (*a%*) – arbuscule richness in root fragments where arbuscules were present (Trouvelot *et al.* 1986). The parameters of AM colonisation were described for a sample of the roots of ten individuals.

In addition to the mycorrhizal colonisation parameters, the number of various structures – arbuscules, vesicles and coils was also counted in each sample.

The results of AM colonisation were related to the soil variables on each site where root samples were collected and were related to plant height, width and the length of the longest leaf, the number of flowers and the number of fruits per plant of *I. parviflora* individuals (Chmura, Gucwa-Przepióra 2012).

An alternative statistical approach was used in this work. In the paper by Chmura and Gucwa-Przepióra (2012), the association between the morphometric traits of individuals and AM colonisation was studied using correlation tests between the mean values of the plant traits based on the measurements of ten individuals and AM colonisation indices. Such a procedure leads to the loss of some information about any variations in the plants in a sample. Therefore, in this work all of the individuals that were measured were counted in the correlation matrix data; however, the values of the AM colonisation parameters were pooled (repeated). Only the Spearman rank correlation tests were used because of repeated values. The Bonferroni correction for multiple tests was not applied assuming the argument given by Moran (2003) in order not to omit possible important results.

Research on interactions with coexisting species in the forest floor and other substrata

For the purpose of this research, floristic and vegetation data from both spatial studies on the permanent plots from the Silesian Upland and the Jurassic Upland were analysed as well as data from the long-term research. The species composition of each study plot was compared using Euclidean distance between the years. The median of the biodiversity indices including the number of species, the values of Shannon-Wiener and Evenness were compared using the Friedman tests and the Conover test for pair-wise comparisons, i.e., differences between succeeding years.

The classification of indicator species into two groups of sites –invaded and uninvaded – at 1 m^2 was performed using the indicator value, i.e., the IndVal method (Dufręne, Legendre 1997) as modified by Cáceres and Legendre (2009) and finally improved by Cáceres *et a*l. (2010). The statistical significance of this relationship is tested using a permutation test. This classification was performed separately or specific distinguished vegetation units. Only those indicator species for both groups that had an IndVal higher than 0.6 of the range (0.0-1.0) were taken into account. Habitat overlap and the coexistence and exclusion of *Impatiens parviflora* and accompanying species across plant associations were tested by calculating the Spearman rank correlation coefficients between the cover of *I. parviflora* and the cover of the most common coexisting species. The correlations were performed separately for all of the study plots combined from the nature reserves of the Silesia Upland and for the study plots of the Jurassic Upland.

Any changes between the abundance of *I. parviflora* and the most abundant species in the herb layer in the particular study plots in the Jurassic Upland were analysed by comparing the values of the Spearman rank correlation coefficients between the covers of the species in respective years.

The following microhabitats were included in the analyses for research on relations between *I. parviflora* and accompanying species in the microhabitats that were associated with dead wood – the area near a log; hollow; log under a canopy; log under a canopy opening; root plate; stump and tree fall disturbance. The association between the density of *I. parviflora* and the number of native species and their total density was tested using the Spearman rank correlation test. To measure the density of other accompanying species, the number of shoots, leave rosettes or clumps that were due to the life form of a species were used. The density was calculated as the total density of plants per unit of area (1 m^2). The density was correlated with cover (see paragraph *Spatial and temporal variation in life history* in Chapter 2.3 Population Studies). Rarefaction gave similar results, e.g., (Chmura 2008c).

2.7. Data processing

The choice of tests that were used for statistical analyses was made due to the character of data. Non-parametrical tests were performed for the ordinal and categorical data. In each case percent of cover was treated as ordinal data because it was derived from a visual estimation. Categorical data were analysed using contingency tables, mainly the G-test and less frequently chi-square test. The former is less conservative than the latter. The G-test was used with or without Williams' correction depending on the size of the samples and the presence of zeros. When the data were of an interval scale, then the distribution of normality was checked using the Shapiro-Wilk, Kolmogorov or D'Agostino-Pearson tests. The homogeneity of variance was checked using the Levene test (Sokal, Rohlf 1995). For convenience and clarity, in some cases the descriptive statistics were presented as means ± SD (instead of medians) or simply as arithmetic means as in the case of the analysis of life traits in time. Statistical analyses were conducted chiefly using the R language and environment (several versions), (R Development Core 2012) and with some exceptions: Pop Tools (Hood 2011), PAST (Hammer *et al.* 2001) and contingency tables software (Legg 2004b). The majority of the ordinal analyses, PCA, RDA and DCA, were conducted using CANOCO 4.5 software (ter Braak, Šmilauer 2002). An alpha level of significance at $p < 0.05$ was accepted throughout the entire work.

3. Results and discussion
3.1. Biotopic requirements of species
3.1.1. Diversity of substratums and soil conditions
Ecological amplitude

The species tends to be more frequent on "cold" slopes, i.e. northern-facing (N, NE, NW) than on "warm" slopes, i.e. southern-facing (S, SW, SE) (Fig. 4). The former contribute 38.7% to all slopes, the latter – 25.8%. The majority of the stands of small balsam in forests are sites where the litter depth varies between 1-4 cm – almost 51% followed by a litter depth of between 4 and 6 cm (27%) (Fig. 4).
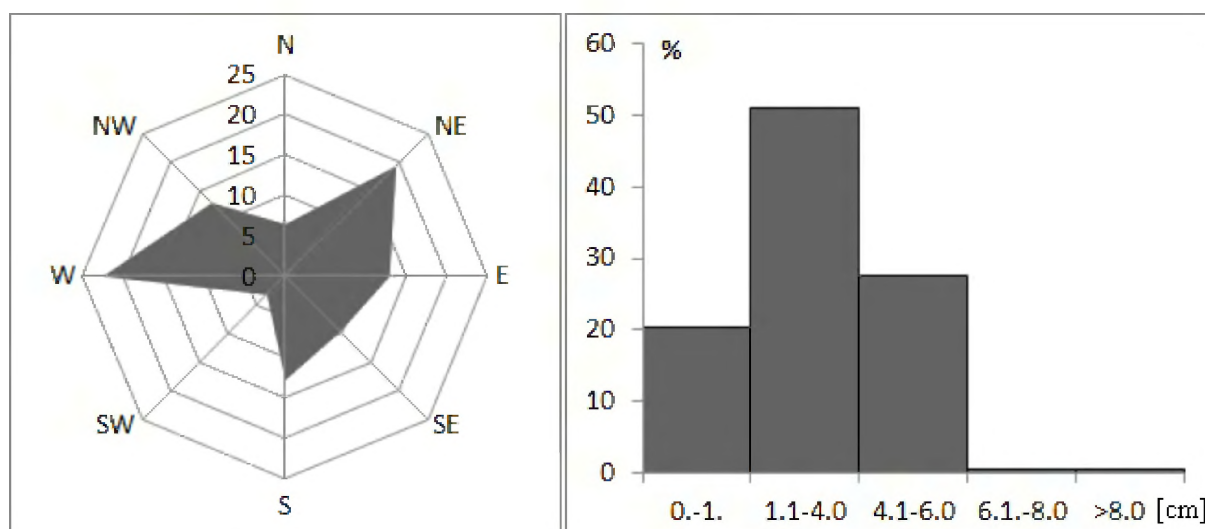
Fig. 4. Aspect of the sites and the litter depth on sites with *Impatiens parviflora*
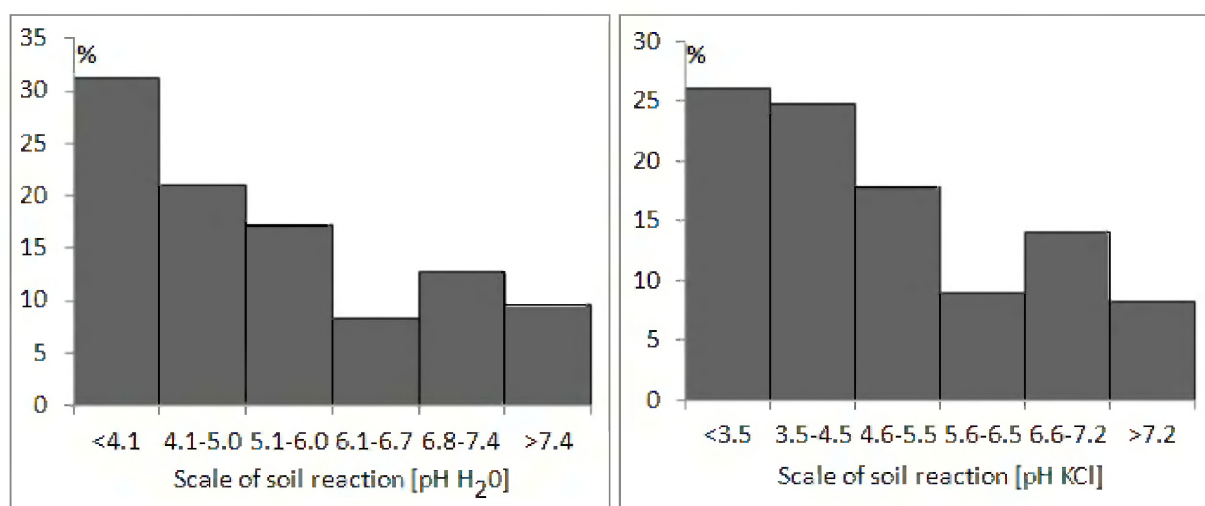
Fig. 5. Variations of soil pH on the sites with *Impatiens parviflora*

Almost 70% of all of the stands that were studied are sites with definitely acid soils (very strongly, strongly and acid); only 30% are slightly acid, neutral and alkaline habitats both in terms of pH in the water and in pH in KCl (Fig. 5).
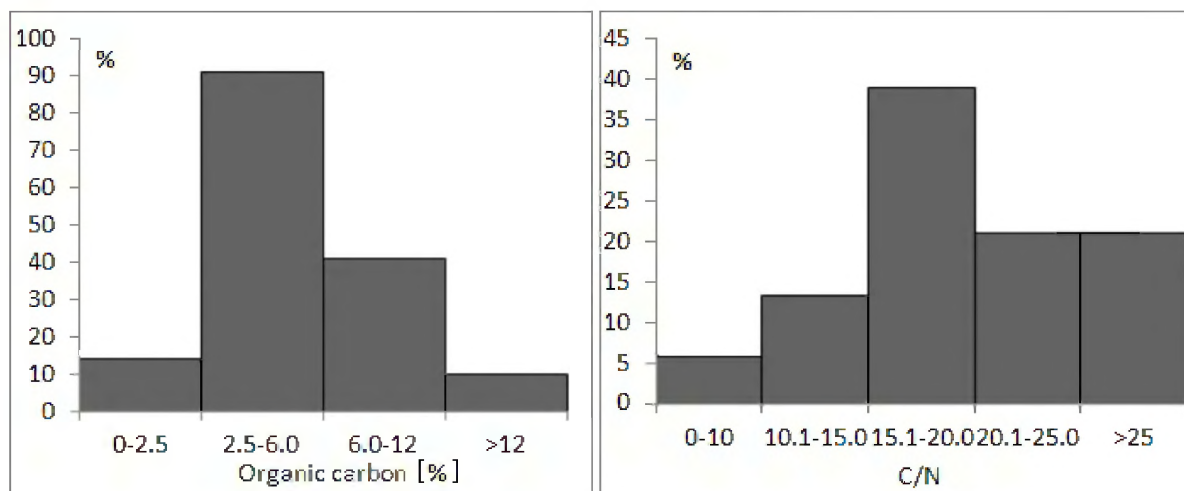
Fig. 6. Variations in the organic carbon and C/N on the sites with *Impatiens parviflora*

Impatiens parviflora prefers sites with an intermediate concentration of organic carbon (Fig. 6). The majority (i.e. almost 40%) of the sites represent a moder type of humus (Fig. 6).
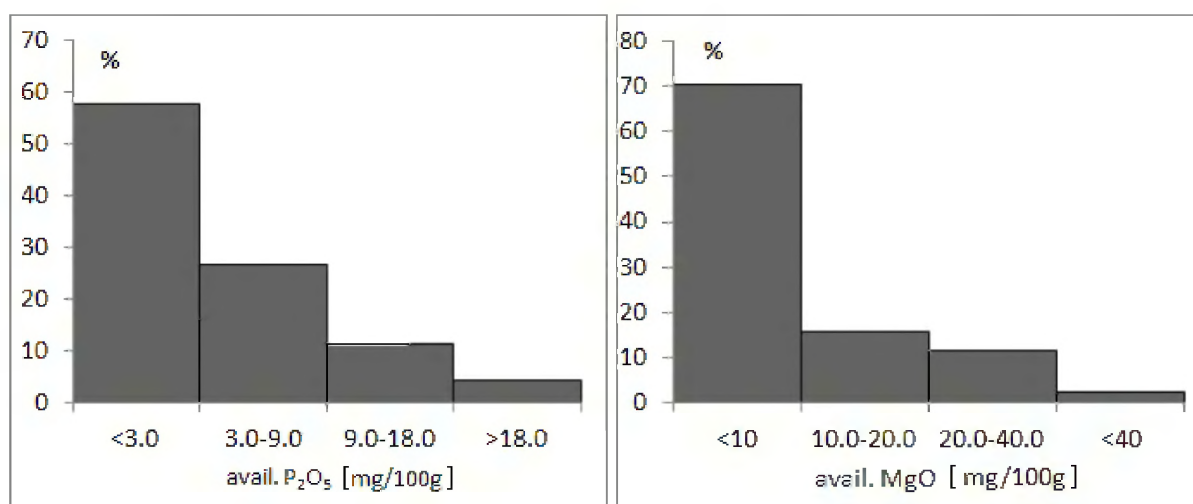
Fig. 7. Variations in the amount of available phosphorus and magnesium on the sites with *Impatiens parviflora*
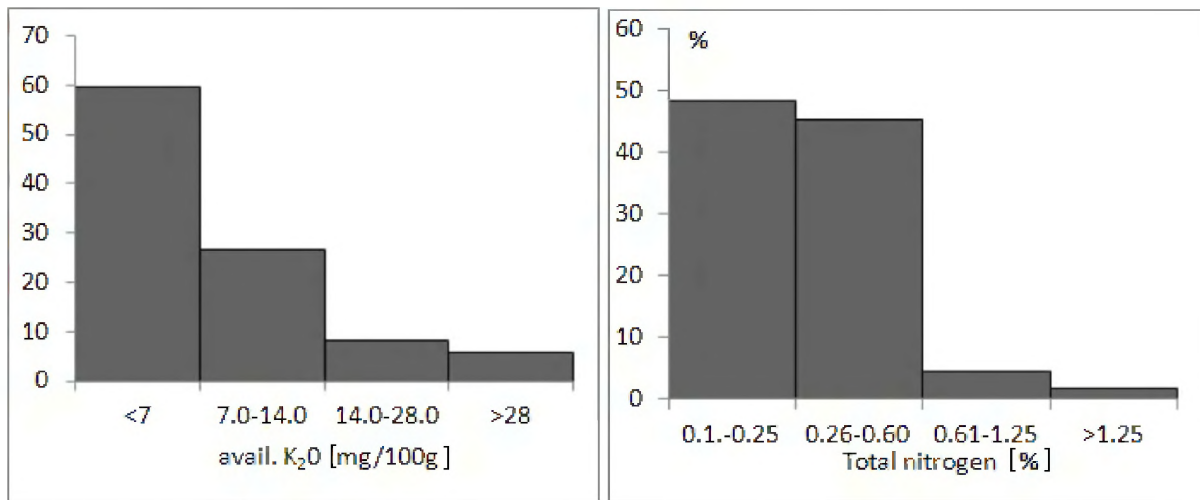
Fig. 8. Variations in the amounts of available potassium and total nitrogen on the sites with *Impatiens parviflora*
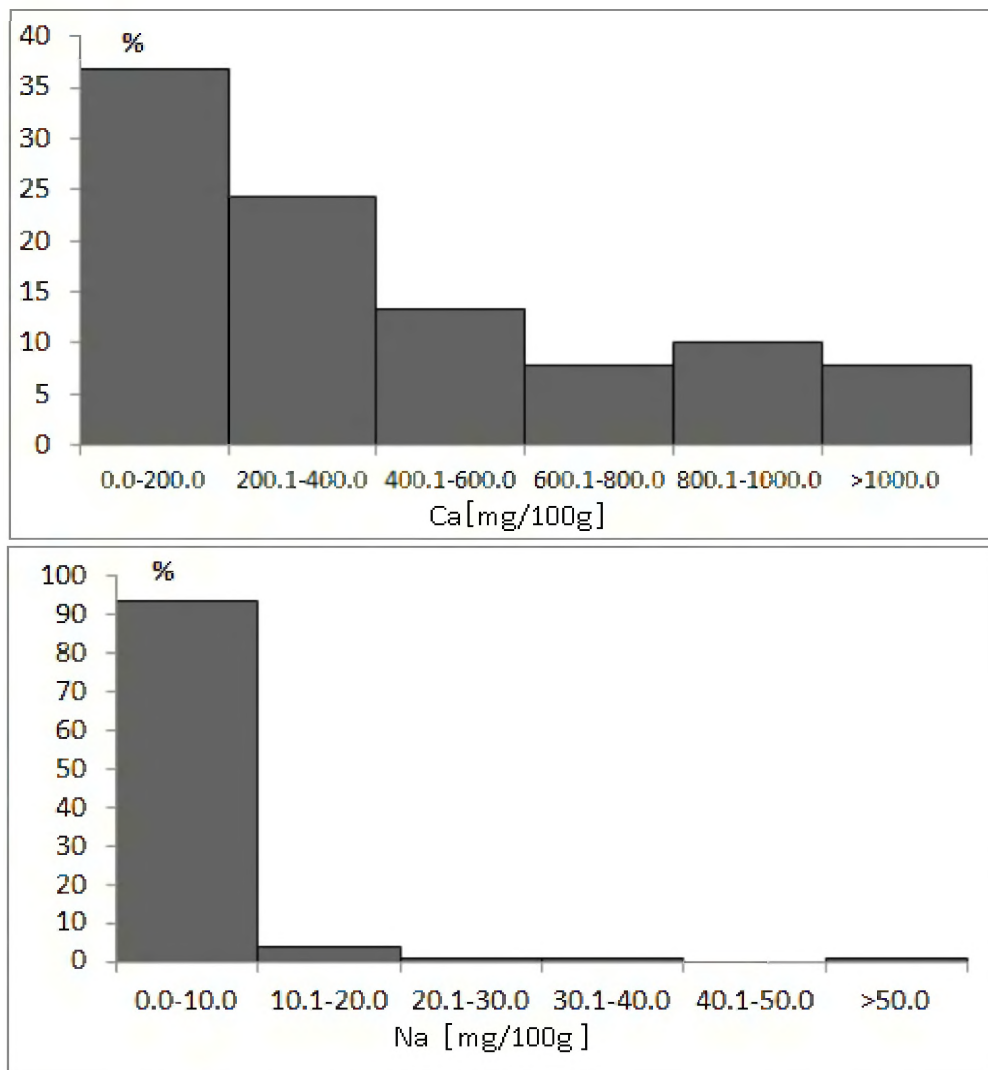
Fig. 9. Variations in the amounts of calcium and sodium on the sites with *Impatiens parviflora*

As far as the trophy, which is characterized by the concentrations of available phosphorus, magnesium, potassium and total nitrogen, is concerned, sites with the presence of small balsam are rather poor (Fig 7-8). More than half of the sites are located in the lowest classes of particular scales. See Table 2 for a comparison. The content of calcium indicates that soils that are occupied by *I. parviflora* are rather poor or intermediate rich in Ca^{2+} ions in this area (Fig. 9). Soils also are very poor in relation to their content of sodium (Fig. 9).

The loss on ignition is rather low and almost 90% are contributed by the two lowest classes in the scale (Fig. 10). Variations in the participation of floatable parts in the granulometric composition are interesting.
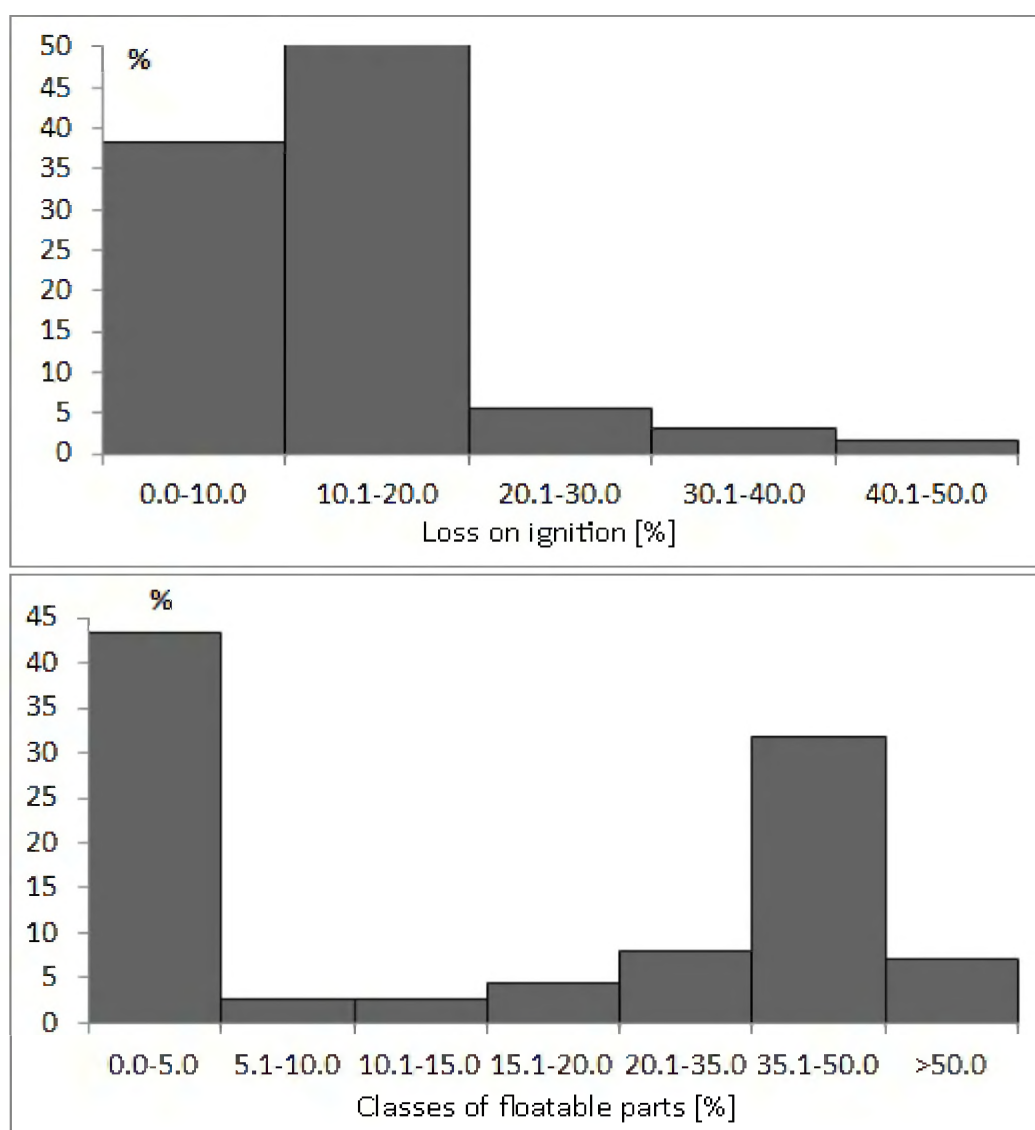
Fig. 10. Variations in the loss on ignition and the percentage of floatable parts in the granulometric composition of soils on the sites with *Impatiens parviflora*

There are two peaks – participation of less than 5.0% in a soil sample is the most frequently represented (ca. 43%); another quite abundant contribution (ca. 35%) is for a class that varied from 35.1-50% of floatable parts in the soil (Fig. 10).

Since the work by Brothers and Spingarn (1992), many studies have revealed that some species prefer southern-facing and that others prefer northern-facing slopes. Godefroid *et al.* (2003) showed that species tend to be more frequent on eastern slopes. Coombe (1956) claimed that small balsam is more abundant on the northern-facing slopes but only when there is less shade. Indeed, in the initial stages of an invasion, small balsam was found on northern slopes (Csontos 1986). In their ordination analysis, Ling and Asmore (1999) found that small balsam is generally associated with steeper slopes but they did not specify the aspect. Previous studies conducted only in the Jurassic Upland (Chmura 2006) or those performed on a larger area that included a smaller number of sites in the analysis demonstrated similar results (Chmura *et al.* 2007) and showed a preference for northern slopes. In a recent work that included an analysis of indicator species, Godefroid *et al.* (2006) proved that small balsam is confined to northern slopes to a significant degree. As regards litter thickness, Coombe (1956) wrote that litter decomposition and nitrification is active but mentioned nothing about the thickness of litter although it can be concluded that sites with litter are preferred by the species.

Węglarski (1991) showed that the roots of *I. parviflora* can grow down to a depth of 12 cm and therefore litter should not pose a barrier for species establishment.

The frequency of *I. parviflora* on sites that differed in soil parameters were analyzed by Węglarski (1991) who used his own ecological indicators values to study the ecological amplitudes of species that occur in the Wielkopolski National Park. According to his research, small balsam is an indicator of weakly acid and acid soils that are rich in phosphorus and potassium and very rich in humus. As for the percentage of floatable parts, soils were classified as sandy clays and clays. The present results confirm that small balsam is confined to soils with lower pH; however, it seems that there are two optima. The majority of stands are characterized by lower contents of phosphorus and potassium, which is in contrast to Węglarski's (1991) study. Indeed, soils that were occupied by the species can be classified as loose sands (less than 5.0% of floatable parts) and the second most optimum are medium clays (35%-50%). Thus, the present study partially confirms this.

Vervoort *et al.* (2011) analyzed the habitat overlap of small balsam and congener *I. noli-tangere* based on 13 sites with deciduous and coniferous forests in Belgium. What is interesting is that there were no differences between the two species, but no comparison was

done with *Impatiens* sites. Sites with *I. parviflora* had higher pH than uninvaded sites (5.2 vs 3.0) and higher concentrations of magnesium and potassium (1285±446 cmolc kg - 1554±108) vs non-occupied sites (98±20, 112±10), respectively. Those results are contradictory to those presented in the study but this should be treated with caution because of the different methods that were applied. Both ecodiagrams with *a priori* assigned classes of particular variables and a comparison of invaded and uninvaded sites in a limited area can give different and biased results. An analysis of the environmental requirements of species that takes into account its abundance seems to be more reliable.

Relationship between abiotic parameters and species abundance

Four soil parameters are significantly and positively correlated with the cover-abundance of *I. parviflora* (Fig. 11).
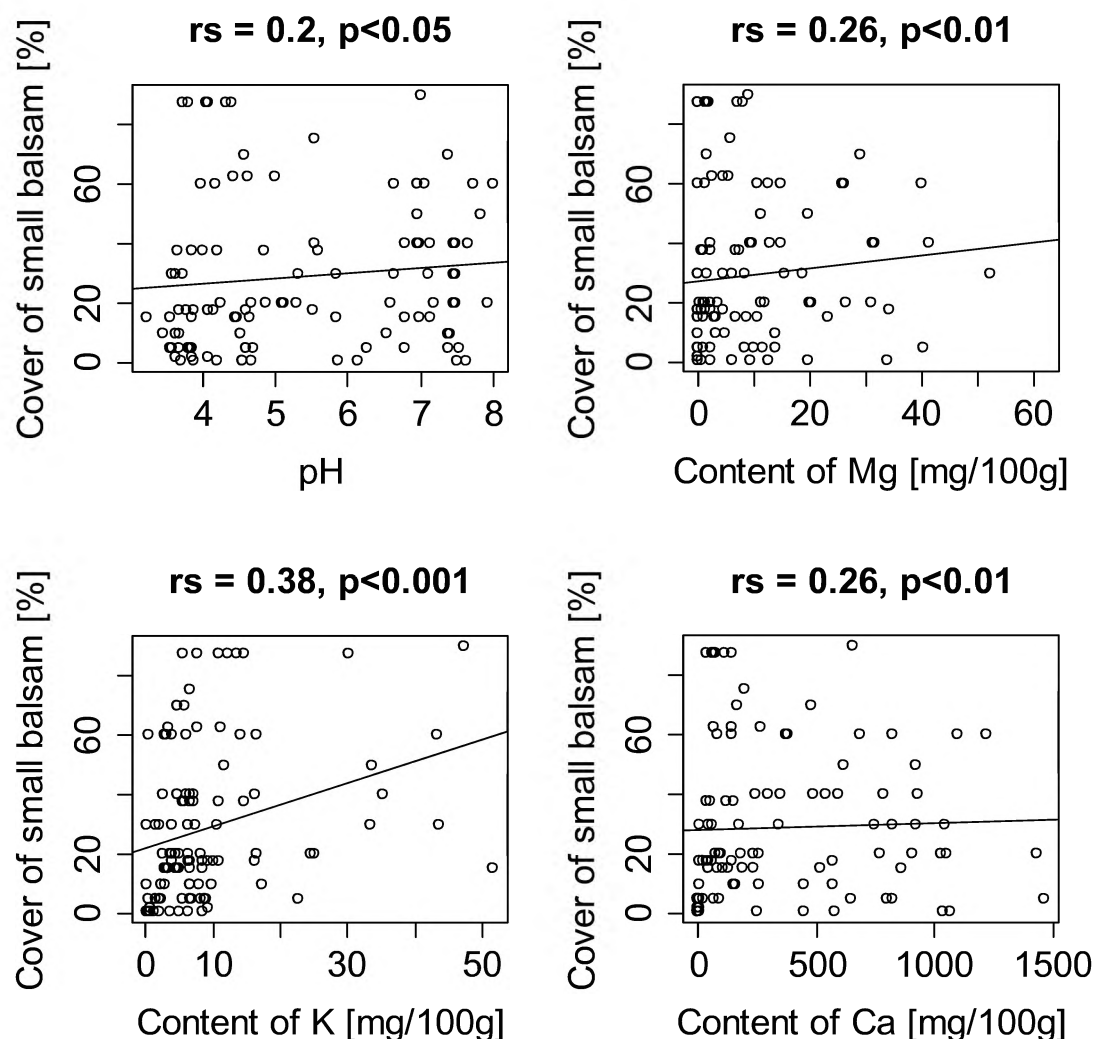

Fig 11. Results of the Spearman rank correlation (r_s) between the cover-abundance of *Impatiens parviflora* and the properties of soils

The strongest and medium correlation was with the concentration of potassium and the remaining ones with magnesium and calcium have a medium and weak correlation with pH. Despite the fact that the ecodiagrams showed that sites with the presence of *I. parviflora* were typified by low contents of magnesium, potassium and calcium (Fig. 7-9), analyses of the abundance of the species and the content of the elements in substratum produced opposite results.

Dobravolskaite (2012) showed that a lower density of *I. parviflora* was observed on soils that were poorer in nutrients and that sites with rich humus soils had a higher number of plants. The correlation analysis is more in agreement with the above mentioned results by Vervoort and Jacquemart (2012). In their study, the presence of species was typified by a higher concentration of nutrients, and in this study the cover of small balsam also increases with increasing values of some nutrients. Dyguś (2008), who investigated the effect of fertilization on changes in vegetation and the concentrations of nutrients in the organs of plants, stated that *I. parviflora* is a potassium-demanding plant. Despite the fact that his was a different type of research, his finding corresponds to the present study, which showed a positive correlation with potassium. Čuda *et al.* (2014) indicated that moisture was negatively correlated with the cover of small balsam, whereas tree cover was positively correlated. In the present work, a negative correlation (r_s= -0.07) with moisture was revealed but it was non-significant. No significant relationship with nitrogen content was detected in the present study. Buriánek *et al.* (2013), when analyzing phytosociological and soil data in the Czech Republic, did not find significant changes in *Impatiens parviflora* coverage due to the nitrogen content in soil in either the humus and M01 (0-10 cm) and M12 (10-20 cm) layers. However, with a decreasing value of C/N in humus and M01, M012: 0-10 cm and 10-20 cm, the cover of small balsam significantly increased. Ratio of carbon to nitrogen is considered as a good evidence of nitrogen saturation in ecosystem (Burianek *et al.* 2013, Aber *et al.* 1989). The lowered value of C/N indirectly indicates demand of the species for nitrogen and therefore *I. parviflora* can be considered as nitrophilous species. Moreover, it is known that input of nitrogen into soil may cause increase of cover of small balsam as in the research in oak pine by Turnau *et al.* (1992). The other important thing is that total nitrogen content perhaps, which did not showed significant result in the present study, is not a good measure to investigate plant responses to nitrogen in soil. The available forms of this element for plants are ions NH_4^+ and NO_3. The evidence for unfit of total nitrogen for such analyses was given by Rahmonov *et al.* (2013) who studied soils from pine forest, river banks to colliery waste tips overgrown by *Reynoutria japonica* no significant differences in total nitrogen content was

exhibited. Kupcinskiene *et al.* (2013a) showed that eutrophication of the environment, especially in anthropogenic habitats, is an important factor in the spread of alien *Impatiens* spp including *I. parviflora* in the Baltic regions. Moreover, the uptake of heavy metals also does not hinder an invasion of this species.

As regards soil reaction, there are ambiguous data because Macková (2012) obtained opposite results the number of individuals decreased at higher pH.

3.1.2. Phytoinidication of the patches of the communities with a contribution of small balsam

The mean Ellenberg indicator values EIVs, which were calculated on the presence/absence data, differ from those EIVs that were originally assigned to *Impatiens parviflora* (Ellenberg *et al.* 1992) (Fig. 12). The differences concern, among others: L - original value light = 4 vs calculated value mvL = 5.12; moisture F =5.7 vs mF = 5. The remaining calculated values for other Ellenberg indicator indices are lower than the original values.
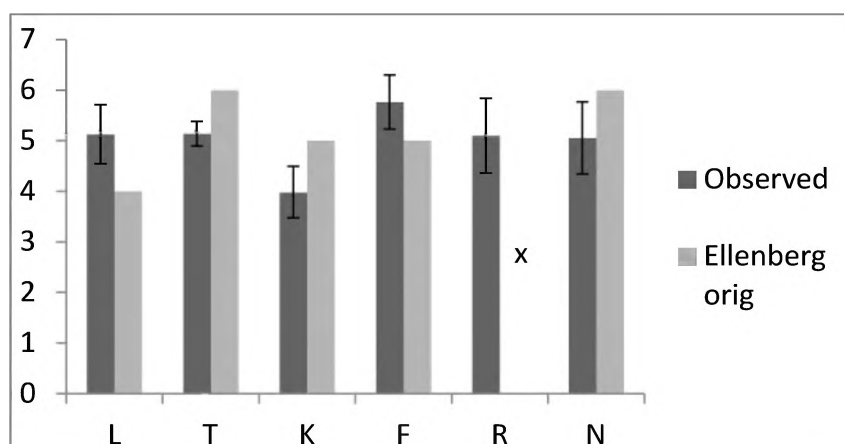
Fig. 12. Original Ellenberg indicator values vs the obtained EIVs (Means±SD) for the Silesian Upland

According to Ellenberg *et al.* (1992), *Impatiens parviflora* is indifferent as to its tolerance to soil reaction. For the sites in the Silesian Upland, mR = 5.09 and it is also characterized by the highest value of the variation coefficient cv =14.5%.

 The EIVs were calculated for *I. parviflora* from five sites in the Czech Republic (Čuda *et al.* 2014). The mean mL was 4.52, which was an intermediate value between the original value of L and mL for Silesian Upland, while the moisture mF in the Czech Republic was almost equal, i.e. 5.72 vs 5.76 and soil reaction was higher mR 5.87 vs 5.09. The nutrient content

espressed by mN for the Czech Republic was also higher (6.48 vs 5.05). These results showed that the soils in this area are poorer than those that are most prefered by the species. Chmura and Urbisz (2005) demonstrated differences between two adjacent regions – the Silesian Upland and the Jurrasic Upland in southern Poland using EIVs as well as between regions but only for particular plant communities. These findings were confirmed by the differences in the soils that were studied among these two mesoregiones and the Glubczyce Plateau (Chmura *et al*. 2005). The EIVs were used to study a comparison of the responses of native *Impatiens noli-tangere* and *I. parviflora* in the forests of Belgium (Godefroid, Koedam 2010). The optimal EIVs for small balsam were as follows: mL = 3, mF = 4, mN = 3 and mR = 4.5. The authors highligtened that their results were not in accordance with the original data as *I. parviflora* turned out to be a more shady plant that prefered more acidic and nutrient poor soil conditions. After recalibrating the indices for the British Isles, Hill *et al*. (1999) obtained a relatively high value for nutrients (N=8).

It is interesting to what extent differences in EIVs indicate differences in the environmental conditions, the responses of the ecotypes of *I. parviflora* or the accuracy of methods that are applied.

The results of the calibration of the calculated EIVs with environmental measurements showed that the correlations are positve and medium for the sites with *I. parviflora* in the Jurrasic Upland but for the Silesian Upland only the soil reaction mR and ph_$H_2$0 are significantly correlated. The remaining correlations turned out to be non-significant despite the fact that a larger sample had been used in the analyses in the case of the Silesian Upland (Tab. 5).

Tab. 5. Spearman rank correlation coefficients between the Ellenberg acidity reaction value mR and the chosen environmental viariables

Variables	mR (SU)		mR(JU)	
	rs	p	rs	p
pH aqua	0.32	0.05	0.40	0.02793
pH KCl	0.28	ns	0.39	0.03397
Ca	0.30	ns	0.42	0.02189
Number of plots	38		30	

SU – Silesian Upland, JU – Jurassic Upland

Many studies have demonstrated a high correlation of the mean Ellenberg indicator values with the measured variables (Dzwonko 2001 and literature cited therein). Most of the calibrating studies of EIVs using field measurements have been conducted for forest

communities (e.g., Diekman 1995; Dzwonko, Loster 2000; Dzwonko 2001; Balkovič *et al.* 2012). One of the best predictors is mR, which was proved for many types of ecosystems by Ertsen *et al.* (1998); however, there are arguments that calibrations should take the effect of vegetation type into account (Wamelink *et al.* 2002). On the other hand, it was shown that even in strongly transformed and secondary habitats such as colliery waste tips (Woźniak, Błońska 2009) mR can be a good predictor. In the present study, it was demonstrated that pH of soil was better predicted in one region (Jurassic Upland) than in the other (Silesian Upland). The main reason for this result is probably the difference in the quality of the forests, which is associated with age, substratum and origin. Forests that are located in nature reserves in the Jurassic Upland are characterized by a high degree of naturalness and diversity (Babczyńska-Sendek *et al.* 2005). The location of the majority of them on calcareous hills has meant that they have been preserved in an agricultural landscape that has been untouched by farming practices. The forests in the Silesian Upland, in regard to the degree of synanthropization (*sensu* Faliński 1986), resemble recent forests. The Ellenberg indicator system has already been tested in respect to light, pH_H_2O, total nitrogen, cation exchange capacity (CEC) for ancient and recent forests (Dzwonko, Loster 2000; Dzwonko 2001). This study revealed that EIVs are better predictors of soil parameters in ancient forests than in recent forests. Wulf (2003) identified *Impatiens parviflora* as an indicator for ancient woods, whereas Graae *et al.* (2004) showed that there is no clear preference for ancient or recent forest in the case of small balsam. The answer to the main question of whether invaded forest communities can be predicted by EIVs would be biased by the type of forest that is invaded. Various studies proved that *I. parviflora* can occur in almost all types of forests, especially deciduous ones and that their naturalness and species diversity does not matter. The presence of small balsam as such probably does not affect the reliability of EIVs prediction.

3.2. Life history traits
3.2.1. Diversity of seeds and capacity of germination
Diversity of seeds

The highest mean mass was reported for the population from the Beskid Mts in Poland and the lowest was recorded for the Visegrádi Mts in Hungary (Fig. 13). These populations were distinct from other stands in both countries. The Hungarian population with the heaviest seeds on average was located in a river valley, whereas the population with the lightest seeds in Poland was also observed in the same type of habitat. There are populations in each country that significantly differ, which was new data and contrary to the previous study

(Csontos *et al*. 2012). Differences in the mass of seeds in small balsam between Poland and Hungary were already discussed in that work. The authors pointed out climatic factors: high temperatures and drought as the main drivers of the lower seed mass in Hungary. On other similar research that focused on *Impatiens glandulifera* (Chmura *et al*. 2013) and additionally included Germany climatic conditions were also determined to be the main causes for the variability of seed mass – differences in precipitation and temperature were mentioned. The present study shows that differences can concern not climatic variables but environmental factors and ecotypes as well. Seed mass for *I. parviflora* was reported from 5.69 (Moravcová *et al*. 2010) and 6.862 (Dostál 2010) for the Czech Republic and from 6.91 to 9.0 g of thousands of seeds according to the database of Royal Botanic Gardens Kew (RBG 2008). Such a high variation may be a consequence of morphological plasticity that is associated with the adaptation to local conditions. The two populations with the lightest seeds were from an alder floodplain forest and a margin managed forest with *Pinus sylvestris*. There were no significant differences between wet and more open vs drier and more closed habitats (Student T-test, t=-0.7461, p=0.46). The only factor that explained the differences between the populations was time (t=3.99, p=0.0003617). The populations from which seeds were sampled in 2011 had heavier seeds (0.33±0.04 g) on average than those sampled the following year (0.27±0.04 g). In 2011 a higher mean temperature in summer was noted compared to 2012.
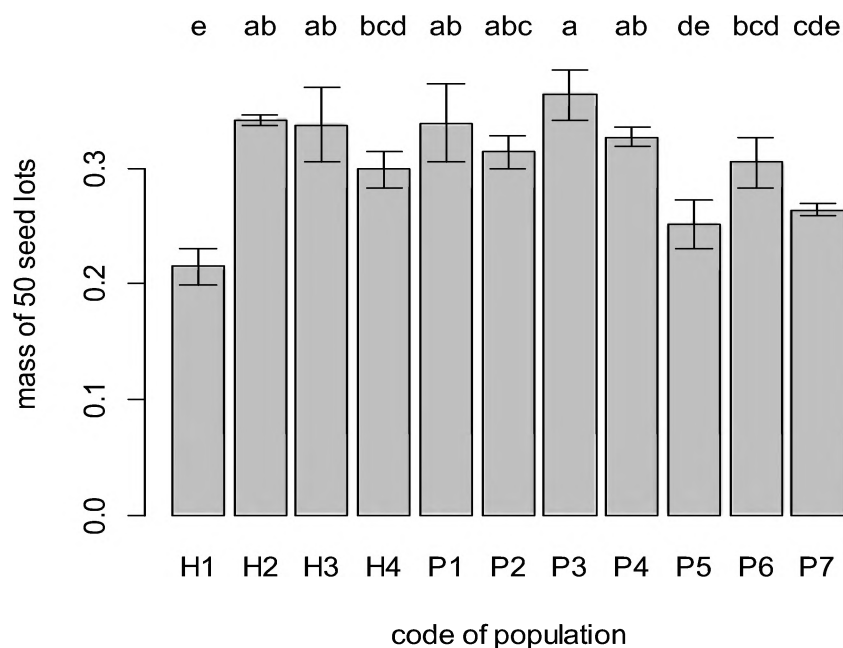
Fig. 13. Comparison of air-dry seed weights among the selected populations of *I. parviflora*. Means ± SE are presented. Different letters above the bars indicate non-significant differences between the samples (ANOVA followed by LSD test). Abbreviations of code of population see table 3

There were serious droughts like those in Hungary so the higher temperature and more light availability positively influenced the ripeness of the fruits and the seeds inside them.

The number of seeds per capsule differed significantly among forest communities (G=103.3, P<0.0001) (Fig. 14). Only one-seed capsules were noted in patches of beechwood *Dentario glandulosae-Fagetum*. In the three other forest communities, this type of capsule was the most frequent reaching 92.5, 87.5 and 90 for an oak-hornbeam forest, an alder forest and a mixed coniferous forest, respectively (Fig. 14). Three and four seeds were only present in capsules in an alder forest and in a population on a forest path. In the latter capsules with two or more seeds were present in more than half of all of the fruits that were measured and analyzed. Csiszar and Bartha (2008) wrote as many as five seeds can develop in capsules; however, no fruits containing five seeds were observed during this study. The majority of capsules had no more than three seeds per capsule although fruits with four seeds were also present, which is in disagreement with the research by Perrins *et al.* (1993), who recorded fewer than three seeds in a garden experiment conducted in the UK. However a similar percentage of fruits containing from one to four seeds was observed in Wielkopolski National Park by Piskorz (2005).
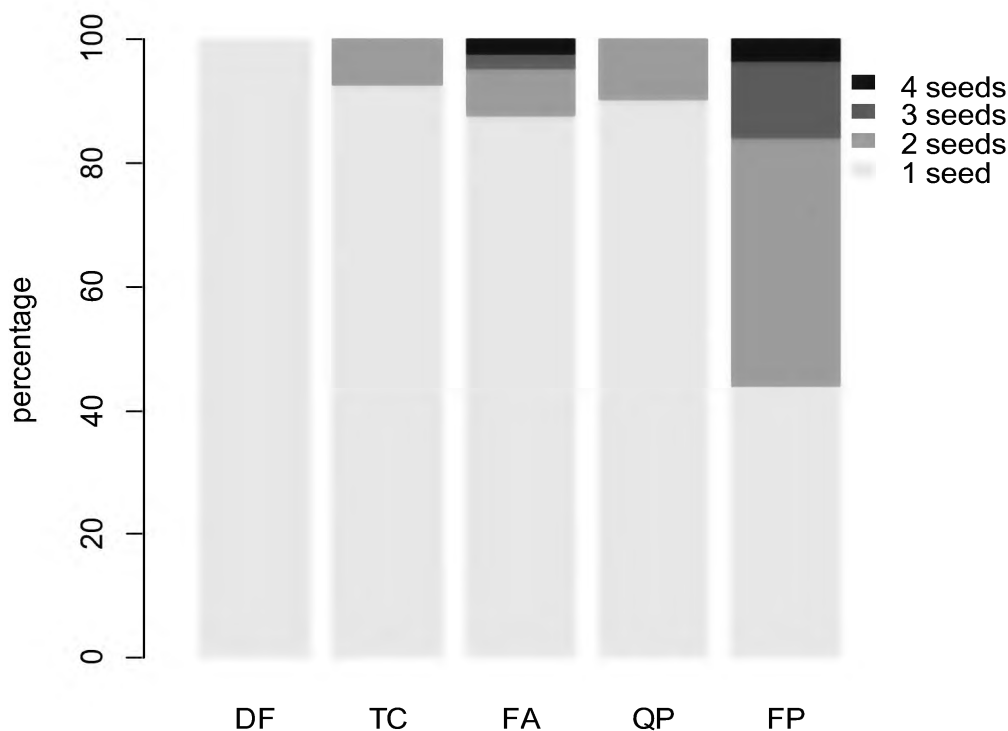
Fig. 14. Comparison of seed production (number of seeds per capsule) between forest communities and the contact zone. DF – beechwood *Dentario glandulosae Fagetum*, TC – oak hornbeam forest *Tilio-Carpinetum*, FA – alder forest *Fraxino-Alnetum*, QP – mixed coniferous forest *Querco roboris-Pinetum*, FP – forest path

Plants growing in canopy gaps had three and four seeds but they were rare 6% and 1%, respectively. In the present study the population in which three- and four-seeded plants were the most abundant grew on a forest path where the light availability was higher and the cover of other plants was lower. The lower number of seeds that was observed by Perrins *et al.* (1993) may be attributed to a different morphological variation caused by climatic factors. Jończyk (2007) studied variations in the dormancy of *I. parviflora* seeds of 11 European populations. The British population was characterized by constantly differing times of germination. It can be expected that some other traits would differ among remote sites.

Germination conditions

A comparison of the different treatments that were applied in the germination experiment revealed that all of the treatments that were used had an influence on the percentage of germination of *I. parviflora* (Tab 6). Detailed data about germination [%] are given in Table 7. On average, 34.5% of seeds for all of the treatments from the forest path habitat combined germinated, followed by the alder forest (25.9%) and the oak-hornbeam forest (21.8%) (Tab. 7).

The mean percentage of germination for all seeds that had been stratified at -2.5°C amounted to 50.7%, whereas the seeds that had been stratified in 3.5°C scored 12.2% on average. The seeds stored at 8.5°C amounted to a mean germination of 37.6% and seeds stored at 20°C germinated at 23.8%.

Tab. 6. Results of the comparison of treatments and types of habitat on the percentage of germinated seeds of *I. parviflora*

	G	P	df
Effect of habitat (only for stratification at 3.5°C and -2.5°C combined)	86.2	<0.0001	8
Effect of stratification temperature (3.5°C vs -2.5°C on all habitats combined)	60.96	<0.0001	4
Effect of storage temperature (8.5°C vs 20°C, for only 3.5°C and -2.5°C of stratification temperature and for FA and TC)	73.70	<0.0001	4
Effect of the time of stratification (for all remaining types of habitat and treatments combined)	516.84	<0.0001	4

Time influenced the germination of *Impatiens parviflora* seeds and the mean percentage of germinated seeds decreased as follows: 40.25% (14 weeks), 38.2% (18 weeks), 37.2% (16 weeks), 9.1% (11 weeks) and 6.7% (9 weeks).

The results that were obtained confirmed previous findings (Kinzel 1912; Coombe 1956, Shaddach 2008; Perglowa *et al.* 2009) that storage of seeds at room temperature without cold stratification causes no germination or that only a few seeds are able to germinate. The present study shows that independent of the habitat from which plants derive a lack of stratification has the same effect (Tab. 7). Kinzel (1912) and later (Coombe 1956), proved that exposure of seeds to temperatures around -5°C enhances the germination percentage. Temperatures of 0-5°C and wet conditions are almost always pivotal for starting germination in this species, which was showed by Jouret (1976).

Tab.7. Percentage of germination of *Impatiens parviflora* in various types of habitat and treatments

Habitat	Temperature of storage	Stratification	Weeks of stratification				
			9	11	14	16	18
FA	20° C	8.5° C	0	0	0	0	2
	20° C	3.5° C	0	0	0	0	10
	20° C	-2.5° C	0	25	70	67	87
	8.5° C	3.5° C	5	10	48	63	52
	8.5° C	-2.5° C	60	54	89	90	85
TC	20° C	8.5° C	0	0	0	0	0
	20° C	3.5° C	0	0	10	18	5
	20° C	-2.5° C	0	2	92	51	40
	8.5° C	3.5° C	0	0	8	12	4
	8.5° C	-2.5° C	0	2	86	45	39
FP	20° C	3.5° C	0	0	0	10	50
	20° C	-2.5° C	15	16	80	90	84

FA – *Fraxino-Alnetum*, TC – *Tilio-Carpinetum*, FP – forest path

This study demonstrated that temperatures below 0° C induced a more abundant and faster germination. Sometimes, natural stratification is not enough (Godefroid *et al.* 2011), and therefore a stable below-zero temperature is needed to induce germination. The same was showed by Komosińska (pers comm., 2008) who demonstrated that seeds germinate earlier when the temperature is lower. Coombe (1956) claimed that seeds younger than six months old never managed to geminate. The present and other studies indicate that germination is possible within a shorter period of time. (Komosińska 2008) demonstrated that 19-week-old seeds are able to germinate. It is not certain what the effect of habitat on the ability to germinate is. Komosińska *et al.* (2006) pointed out that seeds from a floodplain ash-elm forest had a shorter mean time of germination than a population from a ruderal site, i.e. railroad tracks. Indeed, in the present study, plants from the floodplain forest germinated earlier and

the percentage was higher when compared to the oak-hornbeam forest population. Seeds on the forest path were taken from the neighborhood of both forest communities and mixed them. The participation of seeds from the floodplain forest and the effect of light on plants setting seeds might have an impact on the results. The seeds used in the experiment probably differed in size and ripeness but as Trepl (1984) revealed in his experiments, the size of seeds did not indicate any differences in germination. Thus, the differences among habitats are caused by the environmental factors that are associated with the sites. Both Jończyk (2007) and Komosińska (2008) believed that due to the maternal effect in the first generation in small balsam, traits including germination features that are inherited from maternal plants that help in their adaptations to new environments. In the present study germination was only performed using seeds that had been directly harvested from habitats that were studied and therefore a possible maternal effect could have occurred.

3.2.2. Morphological variation of individuals

The individuals that were studied had shoots of different heights ranging from less than 10 cm to 125 cm. The shoot heights of the majority of individuals were between 10 and 25 cm. Distribution of this trait was right-skewed and small plants were dominant (Fig. 15A). The distribution of the length of the longest leave was also somewhat right-skewed (Fig. 15B) although there was no real deviation from the normal distribution. A similar pattern was observed in the case of the width of the longest leaf, which was normally distributed (D'Agostino test, p=0.11) (Fig 15C). Both the number of flowers and fruits were similar (Fig. 16AB). Among the individuals that were measured, ca. 20% had no flowers at all and 16.7% did not develop fruits. The majority of plants had fewer than 20 flowers and 20 fruits per plant, which amounted to ca. 85% and 90%, respectively.

Under the conditions of deep forest interiors, the height of plants is much smaller than in open habitats such as forest edges and forest paths, which has been demonstrated in many studies (Coombe 1956; Trepl 1984; Eliáš 1992, 1999; Chmura 2008a; Kujawa-Pawlaczyk 1991; Klimko, Piskorz 2003; Piskorz 2005; Dobravolskaite 2012). Both the percentage of flowering plants and the height of the generative specimens of *I. parviflora* in forest interiors were small (Fig. 15A, 16A).
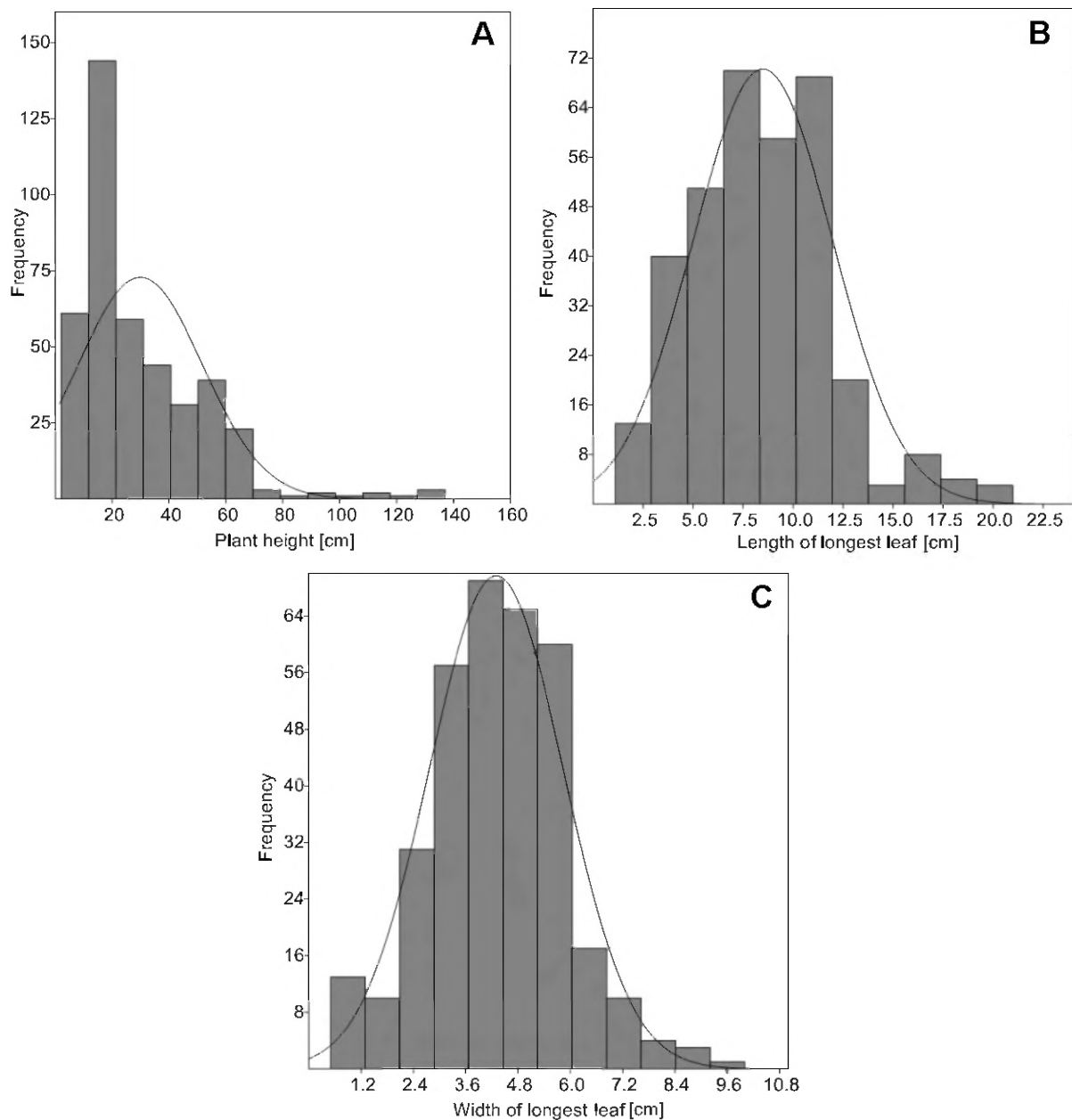
Fig. 15. Histogram of plant height (A), length of leaves (B) and width of leaves (C) with fit of normal distribution (line) based on measurements of 415 individuals
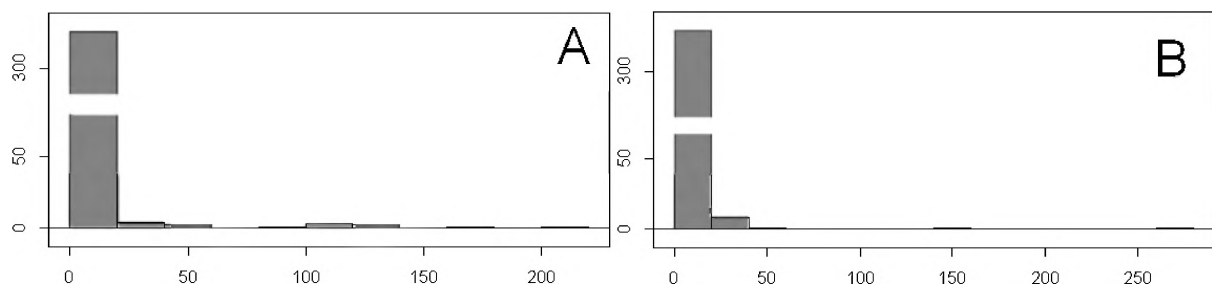

Fig. 16. Histogram of the number of flowers (A) and the total number of fruits (B) based on measurements of 415 individuals growing on mineral soil in forest interiors

Individuals in the blooming phase reached 10-20 cm most frequently, which was mentioned earlier; however, some individuals can even grow up to ca. 140 cm. The frequency distribution was an inverse J-shape. Eliáš (1992) found a J-shape of the frequency distribution for a monospecific stand of small balsam on a clearing along a forest edge on which 60% of the tallest plants (from the upper class of height) prevailed. This diversity might be a consequence of a shift in phenology or differences in environmental factors (nutrients in the substratum, biotic interactions and light conditions). Nevertheless, these results are evidence of a high intrapopulation variation in plant traits in the species. Both the length and width of the longest leaf showed a more normal distribution. These two parameters are associated with leaf area, i.e. they indirectly reflect the photosynthetic ability of a plant. It can be assumed that light conditions with the exception of gaps in the canopy are of a normal distribution and therefore this is manifested in a variation in leaf parameters.

Coombe (1956) wrote that taller plants have more fruits and flowers. In this study non-flowering and non-fruiting plants were in the majority. On the other hand, single individuals had 100-200 seeds per a plant.

The results of Dobravolskaite (2012) suggest that the growth of *I. parviflora* is continuous over time and that it can be expected that the number of generative organs corresponds to the size of plants. However, taking biomass into account like Eliáš (1992) did, the main pattern could be different. It turned out that the tallest plants and those that were dominant within a population of *I. parviflora* allocate more biomass in comparison with codominant and suppressed individuals that are smaller in size. The approximate input of biomass into flowers and fruits reached 9.4%, 7.4 and 6.2% for dominant, codominant and suppressed specimens, respectively (Eliáš 1992).

The acidity of soils was positively correlated with the height of the shoots of *Impatiens parviflora*, although it was a rather weak relationship (Tab. 8). The concentrations of calcium, calcium carbonate, phosphorus and the cover of shrubs were positively correlated with the height of plants.

Neither the length nor the width of leaves was significantly correlated with the parameters of the soils and substratum The number of accompanying species was also not significantly correlated with these parameters (Tab. 8). Only the content of phosphorus, the content of floatable fraction and the cover of shrubs and herbaceous species on the forest floor were positively significantly correlated with the leave traits. The content of total nitrogen and sodium negatively correlated with the number of flowers, whereas total nitrogen positively

correlated with the number of fruits. Slope was negatively correlated in relation to the number of fruits and flowers (Tab. 8).

Tab. 8. Spearman intercorrelation coefficients between the chosen plant traits and environmental variables. Significance at p<0.05 (ns- non-significant)

	stem height	leaf length	leaf width	flowers	fruits
pHaqua	0.15	ns	ns	ns	0.28
pHKCl	0.14	ns	ns	ns	0.30
C org [%]	ns	ns	ns	ns	0.16
C/N	-0.17	ns	ns	ns	ns
Ca [mg/100g]	0.11	ns	ns	ns	0.26
CaCO$_3$	0.16	ns	ns	ns	0.18
K [mg/100g]	ns	ns	ns	ns	ns
LOI	ns	ns	ns	ns	0.15
Mg [mg/100g]	ns	ns	ns	ns	ns
N$_T$	ns	ns	ns	-0.22	0.16
Na [mg/100g]	ns	ns	ns	-0.12	ns
P [mg/100g]	0.28	0.12	0.13	ns	0.23
Floatable fraction [%]	ns	0.13	ns	ns	-0.24
litter depth	ns	ns	ns	ns	ns
Slope	-0.19	ns	ns	-0.15	-0.16
species richness	-0.12	ns	ns	ns	ns
cover of herbs	ns	0.13	0.13	0.16	-0.14
cover of shrubs	0.31	0.13	0.14	0.02	0.40
cover of trees	ns	ns	ns	ns	ns

The cover of herbs positively correlated with the number of flowers but negatively correlated with the number of fruits. The number of fruits per plant revealed many other significant correlations. Acidity, the concentration of organic carbon, calcium ions, calcium carbonate, loss on ignition and phosphorus were all positively correlated although the percentage of floatable fraction was negatively correlated (Tab. 8).

Slope (only for sites situated on hills) and species richness were negatively correlated with the height of plants.

The remaining individuals from forest communities (oak-hornbeam forest, beechwoods and mixed coniferous forest) did not differ significantly in the height of plants. Plants from mixed coniferous forest sites were the smallest and the least productive in the development of flowers, the number of flowers and the length and width of leaves (Fig. 17D). Individuals from the oak-hornbeam forest and mixed coniferous forest had a similar number of fruits (Fig. 17E).
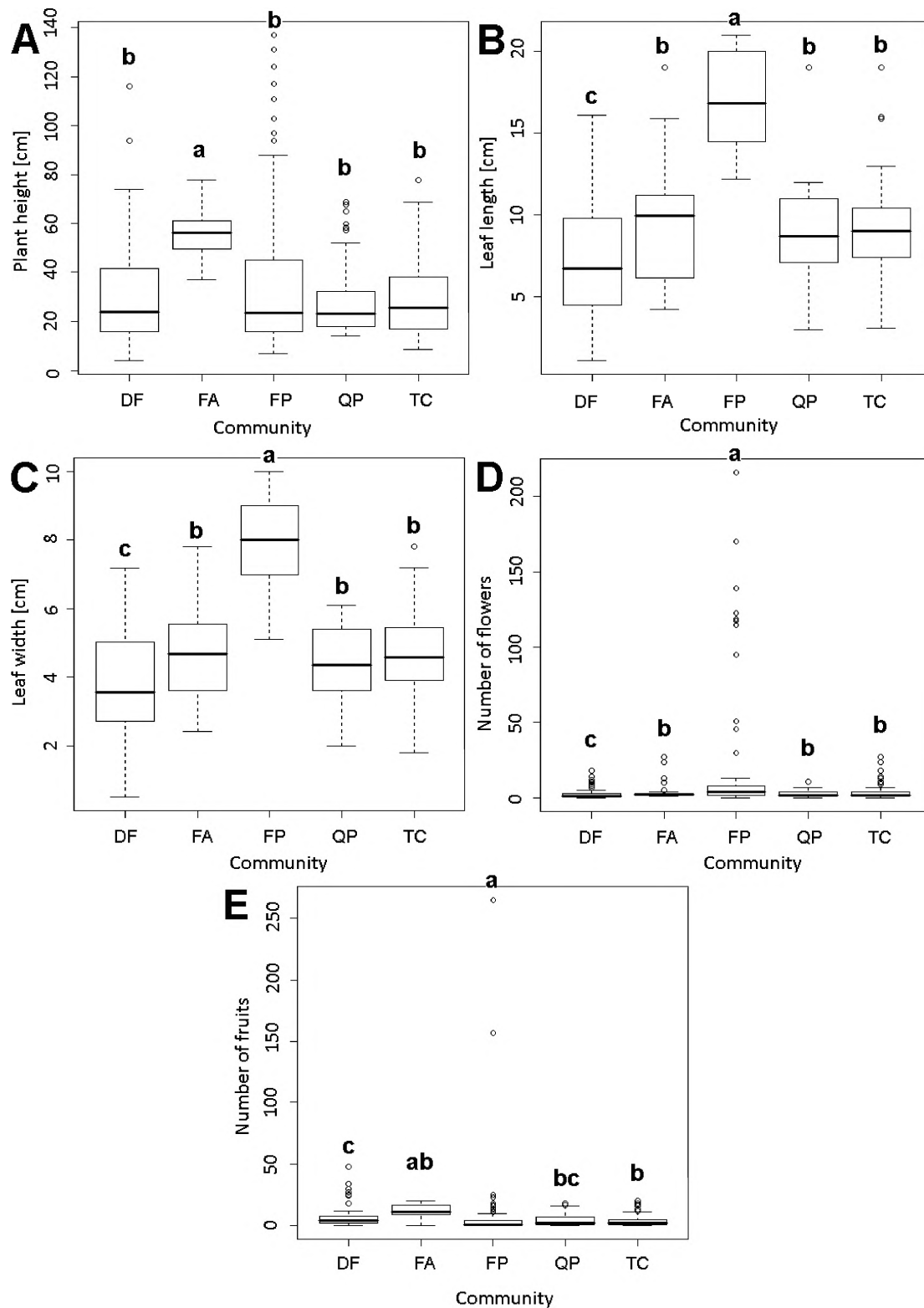
Fig. 17. Comparison of plant height (A) length of leaves (B), width of leaves (C), total number of flowers (D) and total number of fruits (E) per plant in individuals growing on mineral soil in forest interiors. The different letters above the box-whiskers indicate significant differences at p<0.05 (Kruskal-Wallis test followed by Conover test). FA – *Fraxino-Alnetum*, FP – forest path, DF – *Dentario glandulosae-Fagetum*, TC – *Tilio-Carpinetum*, QP – *Querco roboris-Pinetum*

Principal Components Analysis produced five (orthogonal not correlated) components that explain 100% of the variation in the data. According to the results of PCA, the first component accounted for 63% (Tab. 9). Loadings of the first component for the morphometric variables that were used varied between 0.304 and 0.509. The highest value was obtained for the width of leaves, thus this variable is responsible for the highest percentage of variation in the analyzed data. Other important variables are the number of fruits, the number of flowers and the height of plants, which all contributed to the loadings of the following components 2, 3, 4 and 5, respectively.

Tab. 9. The variance and component loadings of particular variables based on measurements of 415 individuals of *Impatiens parviflora*

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5
Proportion of variance	0.603	0.183	0.141	0.061	0.013
Cumulative proportion	0.603	0.786	0.926	0.987	1.000
Flowers	0.405	0.070	**0.791**	-0.453	-0.016
Fruits	0.304	**0.783**	-0.421	-0.342	-0.018
Leaf length	**0.509**	-0.375	-0.274	-0.107	0.716
Leaf width	0.499	-0.411	-0.292	-0.103	-0.697
Height of stem	0.485	0.268	0.192	**0.810**	-0.010

The height of plants usually is associated with enrichment with nutrients. In this study a higher content of available phosphorus, calcium and calcium carbonate influenced the size of plants. Dobravolskaite (2012) revealed that individuals of *I. parviflora* that were growing on humus-rich soil at the edge of a pine forest were the tallest.

The shortest plants were found in the soils that were poorest in terms of nutrients and low pH on sites of the *Picea abies* community. Thus, the results in the present study are in accordance with those that were obtained by Dobravolskaite (2012).

In a previous work by Chmura (2008a), individuals representing populations from different forest and non-forest plant communities (calcareous grassland) and across plant communities that occurred in various habitats (forest interiors, paths, margins, dead logs) were analyzed in regard to the same morphological traits. A greater variation was observed in all of the parameters. The tallest plants were found in a contact zone between an oak-hornbeam and floodplain forest on bare (unvegetated) soil with thick litter. These individuals had many branches of the 3rd order and adventive above-ground roots. The investigated population increased in density but mean height decreased after three years of the study (Chmura npbl). The shortest flowering plants grew on a very thin layer of soil (up to 2 cm) on a limestone

outcrop. It seemed that the thickness of the soil, temperature and full sun conditions were limiting factor for the growth of plants. In contrast, Vervoort and Jacquemart (2011) observed flowering individuals growing in river beds where the water table was 1-2 cm above the root collar. This not only proves very high morphological plasticity but also a very high morphological adaptation to extreme environmental conditions.

Most studies that investigate variations in the morphometric traits of *I. parviflora* focus on differences among the types of habitats within the gradient of naturalness/disturbance, e.g., road-forest borders (Kujawa-Pawlaczyk 1991; Klimko, Piskorz 2003), forest fringe communities (Uherčiková, Eliáš 1987; Eliáš 1992), two forest communities and forest edge (Dobravolskaite 2012) or forest communities and their contact zone with another one (Piskorz 2005). These case studies mainly considered only the size of plants and seldom examined any additional morphometric properties (Piskorz 2005; Dobravolskaite 2012) or plant architecture and biomass allocation (Eliáš 1992). Dobravolskaite (2012) did not find any considerable differences in plant height, plant height up to the first inflorescence or to the first lateral branch in two forest communities – a spruce and a pine forest. Only individuals from the edge of the pine forest had higher values of the parameters. In the present study the four forest communities that were analyzed are much more diversified with respect to habitat properties and structure and plant composition and therefore the differences in the selected plant traits that were observed were significant (Fig. 17). The highest variation and the highest outliers in the height of plants that were growing along a forest path can be explained by the border effect. This phenomenon is known in *Impatiens noli-tangere*, which grows more abundantly in the ecotone between a forest and meadow. The border effect can be manifested by larger plants and higher fecundity (Falińska 2004). There are diverse biotopic conditions along forest paths. Light conditions are poorer on sites that are closer to a dense forest than on more open sites. In each case individuals from the *Fraxino-Alnetum* community had higher values of the plant traits that were studied. Floodplain forests (*Ulmenion* alliance) are prone to invasion due to the sufficient amount of light in the forest undergrowth as well as nutrient-rich soil (Petrášová *et al.* 2013). Knowing the biotopic requirements of the species, it is not surprising that small balsam achieved the highest degree of robustness in the patches of this type of forest. In contrast to that forest, *Querco roboris-Pinetum* plants were the smallest in a mixed coniferous forest. The research by Trepl (1984) clarified that *I. parviflora* prefers broad-leaved forests than mixed and coniferous forests. Unfavorable habitat conditions hinder penetration by this species. It can be presumed that the same conditions that influence the frequency and abundance of the species also have an impact on plant traits. The history of

I. parviflora invasion into Poland was clarified in great detail in the Primeval Białowieża Forest (Kujawa-Pawlaczyk 1991; Adamowski, Keczyński 1991; Faliński 1998b). It was reported that *I. parviflora* only naturalized in deciduous forests, i.e. oak-hornbeam and beechwood. The history of the establishment and spread of the species into the Jurassic Upland is not known although it can be assumed that mixed coniferous forests were colonized later than deciduous forests. The differences between oak-hornbeam forest *Tilio-Carpinetum* and beechwood *Dentario glanduloase-Fagetum* have not been identified except for the number of fruits, which might be associated with differences in the phenology of these phytocoenoses.

The variations in the selected plant properties among the four forest communities that had been distinguished are rather stable because the same variables were used by Chmura and Gucwa-Przepióra (2012) even though individuals that were measured for other purposes had similar results.

3.2.3. Seasonal dynamics of *Impatiens parviflora*

All of the phenophases that had been distinguished were observed in the forest habitats that were analyzed, which is shown on Figures 18-22. They differ in the contribution of almost all of the phenophases with the exception of the preflowering phase (stadium with a presence of flowers buds) (Tab. 10).

Tab. 10. Results of the comparison of the participation of phenophases between the forest habitats that had been distinguished (G-test, ns – non-significant)

Phenophase	Time	G	df	p
two-cotyledon phase	16.04-30.05	45.48	12	0.000009
one-cotyledon phase	30.04-30.06	55.38	12	0.0000002
vegetative phase	17.05-22.09	60.30	32	0.0018
preflowering phase	17.05-30.08	27.39	28	ns
flowering phase	17.05-30.08	65.74	28	0.00007
prefruiting phase	17.05-30.08	45.56	28	0.019
fruiting phase	17.05-30.09	83.84	36	0.00001
subsenile phase	17.07-30.09	33.11	20	0.03
senile phase	14.06-30.09	47.39	28	0.012

Plants with one or two cotyledons were present until the end of June. Plants with only one cotyledon appeared in the second half of May. At the end of May, the contribution of two-cotyledon individuals dropped to less than 20% (Fig. 18). The first fully developed vegetative plants appeared at the end of May but mid-June was optimum for this phenophase. Plants were in the blooming phase from the second half of June until the end of August which was also optimum for the fruiting phase. In beechwood community, the two-cotyledon phase lasted from mid-April until the end of May when single plants with two cotyledons were present (Fig. 19). The highest decrease occurred between mid-May and the end of May when the participation of this phenophase fell from 80% to around 10%. The last plants with single cotyledons were recorded at the end of June. The first individuals that had flowers were found in mid-July; however, the first plants with buds were noted a month earlier. Plants were in the fruiting phase from second half of August until the end of month. The first signals of senescence also appeared during that time frame.

Fig. 18. Participation of phenophases and the survival of individuals of *Impatiens parviflora* in the *Tilio-Carpineum* forest community. Abbreviations: 1 – two-cotyledon phase, 2 – one-cotyledon phase, 3 – vegetative phase (stems without flower buds), 4 – preflowering phase (flower buds present), 5 – flowering phase (open flowers present), 6 – prefruiting phase (with unripe fruits), 7 – fruiting phase (with ripe fruits), 8 – subsenile phase (with declined leaves), 9 – senile phase (stems without leaves)

Fig. 19. Participation of phenophases and the survival of individuals of *Impatiens parviflora* in the *Dentario glandulosae-Fagetum* forest community. Abbreviations: 1 – two-cotyledon phase, 2 – one-cotyledon phase, 3 – vegetative phase (stems without flower buds), 4 – preflowering phase (flower buds present), 5 – flowering phase (open flowers present), 6 – prefruiting phase (with unripe fruits), 7 – fruiting phase (with ripe fruits), 8 – subsenile phase (with declined leaves), 9 – senile phase (stems without leaves)

Fig. 20. Participation of phenophases and the survival of individuals of *Impatiens parviflora* in the *Fraxino-Alnetum* forest community. Abbreviations: 1 – two-cotyledon phase, 2 – one-cotyledon phase, 3 – vegetative phase (stems without flower buds), 4 – preflowering phase (flower buds present), 5 – flowering phase (open flowers present), 6 – prefruiting phase (with unripe fruits), 7 – fruiting phase (with ripe fruits), 8 – subsenile phase (with declined leaves), 9 – senile phase (stems without leaves)

During the study 80% of plants died out from mid-April until the end of September (Fig. 19). The first single senile plants appeared in mid-June, despite the fact that no subsenile phenophase had been recorded prior to that date. Almost 30% of individuals survived until the end of the research (Fig. 19). Only two cotyledons individuals were present at the beginning of the research but half a month later one plant in the one-cotyledon phase was observed. The optimum for this phenophase was at the end of May. The contribution of the vegetative phase was similar to the plants in the *Tilio-Carpinetum* community. The participation of plant that represented the preflowering and flowering phases differed in the optimum periods from the other plant communities. These plants were flowering over a period of two months from June 30 until August 30. The optimum fruiting phase occurred in August and September. The first subsenile plants were observed in mid-July and the highest percentage occurred at the end of August. The survival percentage amounted to almost 36%. The first plants of one cotyledon phenophase after the two-cotyledon phase appeared at the end of April in the mixed coniferous forests (Fig. 21). The optimum time for this phenophase was observed at the end of May. In mid-June ca. 50% of plants represented the vegetative phenophase. The preflowering phenophase lasted quite a long time from mid-June until the end of August.
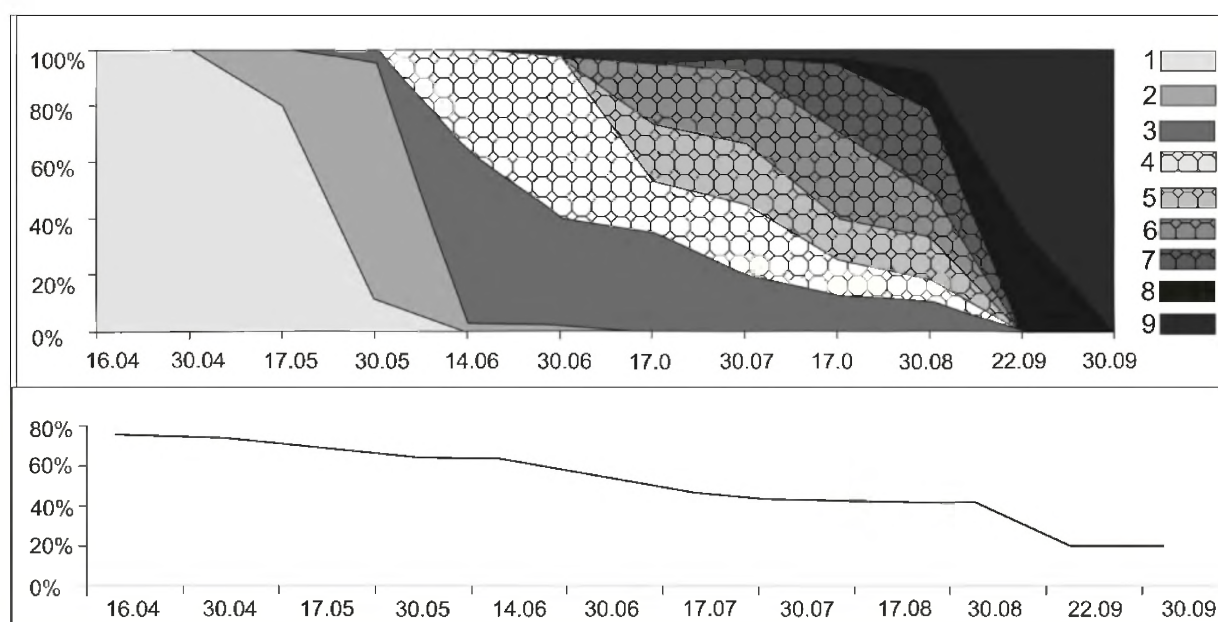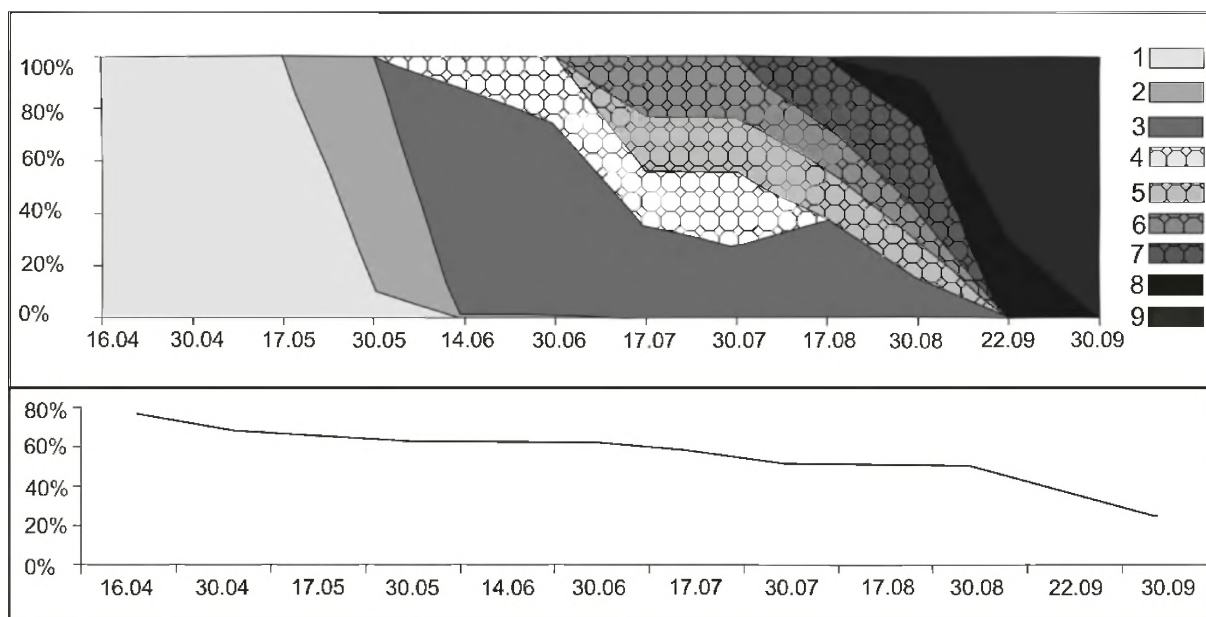

Fig. 21. Participation of phenophases and the survival of individuals of *Impatiens parviflora* in the *Querco roboris-Pinetum* forest community. Abbreviations: 1 – two-cotyledon phase, 2 – one-cotyledon phase, 3 – vegetative phase (stems without flower buds), 4 – preflowering phase (flower buds present), 5 – flowering phase (open flowers present), 6 – prefruiting phase (with unripe fruits), 7 – fruiting phase (with ripe fruits), 8 – subsenile phase (with declined leaves), 9 – senile phase (stems without leaves)
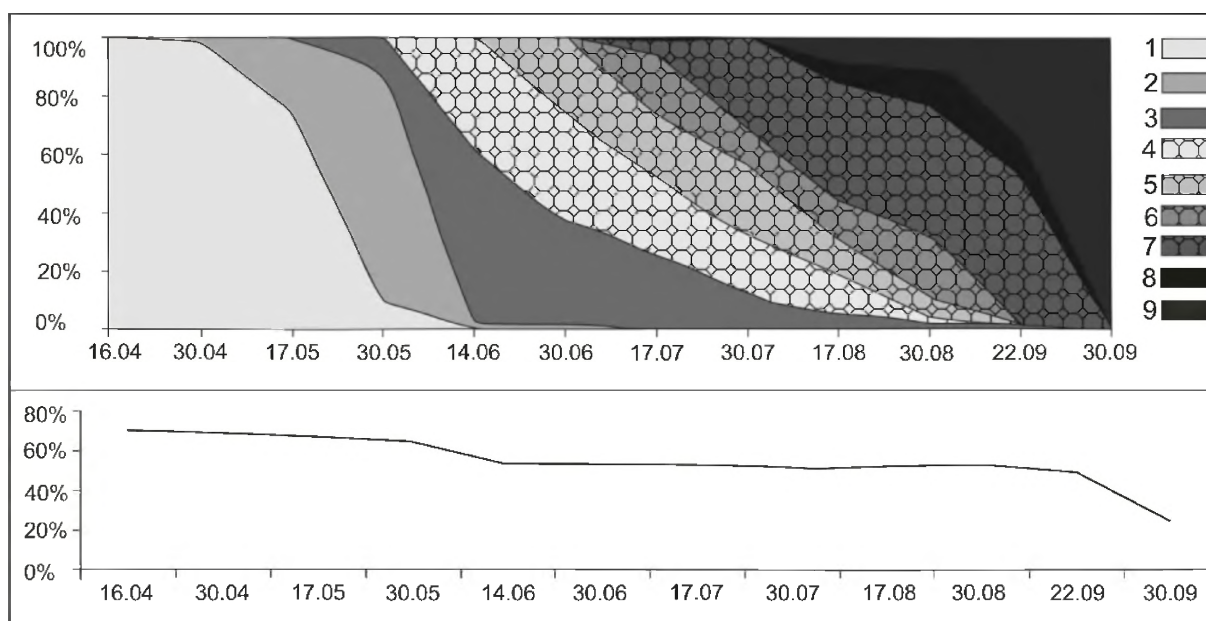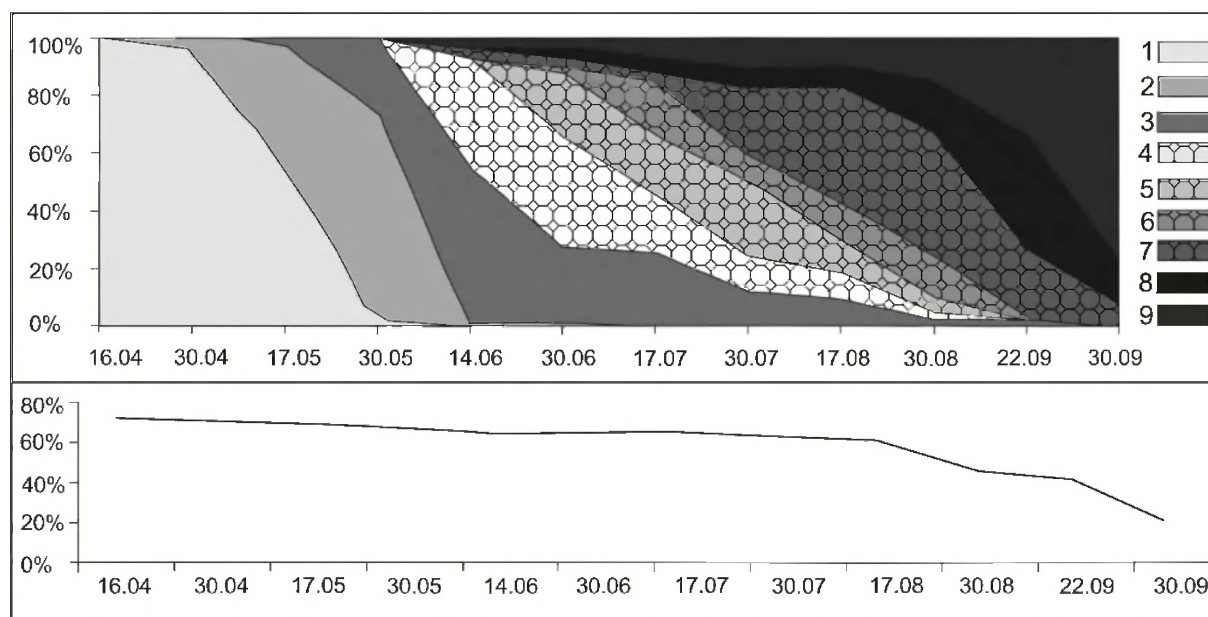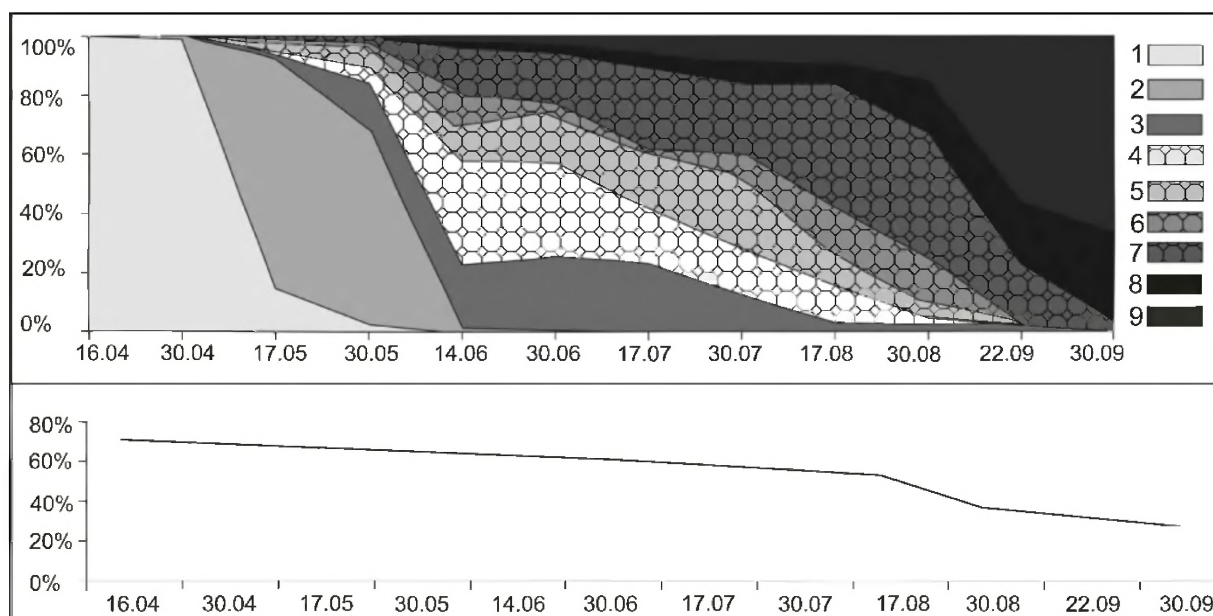
Fig. 22. Participation of phenophases and the survival of individuals of *Impatiens parviflora* in the forest edge community. Abbreviations: 1 – two-cotyledon phase, 2 – one-cotyledon phase, 3 – vegetative phase (stems without flower buds), 4 – preflowering phase (flower buds present), 5 – flowering phase (open flowers present), 6 – prefruiting phase (with unripe fruits), 7 – fruiting phase (with ripe fruits), 8 – subsenile phase (with declined leaves), 9 – senile phase (stems without leaves)

Individuals in the fruiting phenophase existed until the end of the study and its optimum period was the end of August. An early process of senescence was observed beginning in the second half of June. Twenty percent of the labeled plants survived until the end of observation.

The individuals of *I. parviflora* that represented the first two phenophases (one- and two-cotyledon phase) in the forest edge community were present until the end of June (Fig. 22). The vegetative phenophase lasted for quite long time from mid-May until the third week of September. The preflowering phase also lasted for a long time but it ended at the end of August, and the optimum period for this phenophase was at the end of July. The flowering and prefruiting phenophases lasted for the same period of time. The fruiting individuals were present from the second half of May until the end of the research. The period of the subsenile and senile phenophases occurred simultaneously but they differed in the optimum time period (Fig. 22). The percentage of plants that survived dropped to 34%.

Despite the fact that only 12 time series were taken into account, the results of the observations showed significant differences (Tab. 10). This variation is manifested by different optimum periods rather than the time that particular phenophases begin and end. The biggest differences are in the generative phenophases (preflowering, flowering, prefruiting

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and fruiting phases). The plants on the forest fringe sites entered into these phases faster than those in the remaining forest communities.

It is known that there are significant differences in the phenology of *I. parviflora* among different geographical regions. For instance, seeds germinate not sooner than in May in Finland (Erkamo 1952 after Piskorz and Klimko 2002), but in Great Britain seeds are already germinating in March (Coombe 1956). Similar phenological observations, which were the inspiration for present study, were conducted by Piskorz and Klimko (2002) in Wielkopolski National Park. The only differences are related to the number of visits that were made to record the observations and types of forest habitats. Their study was conducted in an oak-hornbeam forest *Galio silvatici-Carpinetum typicum* that resembles *Tilio-Carpinetum* ecologically. Both plant associations are biogeographical variants of the same forest community (Matuszkiewicz 2011). Thus, they can be compared in regard to the contribution of particular phenophases of *I. parviflora* although the authors stressed that their phenological study was conducted in a thinned forest and they also mentioned that the population that was studied was infected by *Puccinia komarovii* – a rust and a natural enemy of small balsam. Moreover, in the present study observations in five habitats were performed in 12 time series while the Piskorz and Klimko (2002) study was conducted every 3-7 days in one community. Nevertheless, some similarities and differences can be observed. First of all, phenophases were present and the time of the beginning of the flowering phase was quite fast. In the present study, it occurred at the end of June but when taking into account the longer breaks between measurements, it can be presumed that the start of flowering phenophase may have occurred earlier. The time of flowering was quite long and lasted until the end of September while the fruiting phase was also quite long and lasted about two months. The phenophases in the beechwood forest were shifted in comparison with the oak-hornbeam forest probably due to its denser tree canopy cover. For this reason, i.e. light availability, most of the differences are between the forest interiors of the investigated forest communities vs the forest path. The first fruiting individuals were found in the second half of May and the earliest senile individuals were recorded at the end of May. Pilkova (2013) compared the participation of phenophases between a forest interior and a forest glade. She noted that the time of particular phenophases was prolonged by a month in an area that had been cut. From the viewpoint of the survival of a population, the most important factor in phenology is the time of special developmental phases. Trepl (1984) believed that such a long period of flowering and fruiting is one of key elements in the invasion success of the species. Several populations that differ in phenology including an extended period of flowering and fruiting have an increased chance of

the persistence of the species when they coexistence in the gradient of a forest interior – forest fringe or forest interior canopy gaps in a specific area.

3.2.4. Life history modifications that are dependent on habitat heterogeneity
Spatial patterns in life history traits

According to the Principal Components Analysis, the first component (axis 1) explains nearly 42% of the variation, whereas the second axis explains ca. 22%. The number of flowers and the height of plants are correlated with the first axis and the number of fruits and the number of flower buds per plant correlate with the second axis. The presence of cotyledons only plays a minor role. PCA showed that some individuals that represented various microhabitats differ from other plants, but the majority of individuals that were analyzed are situated close together on the diagram (Fig. 23).
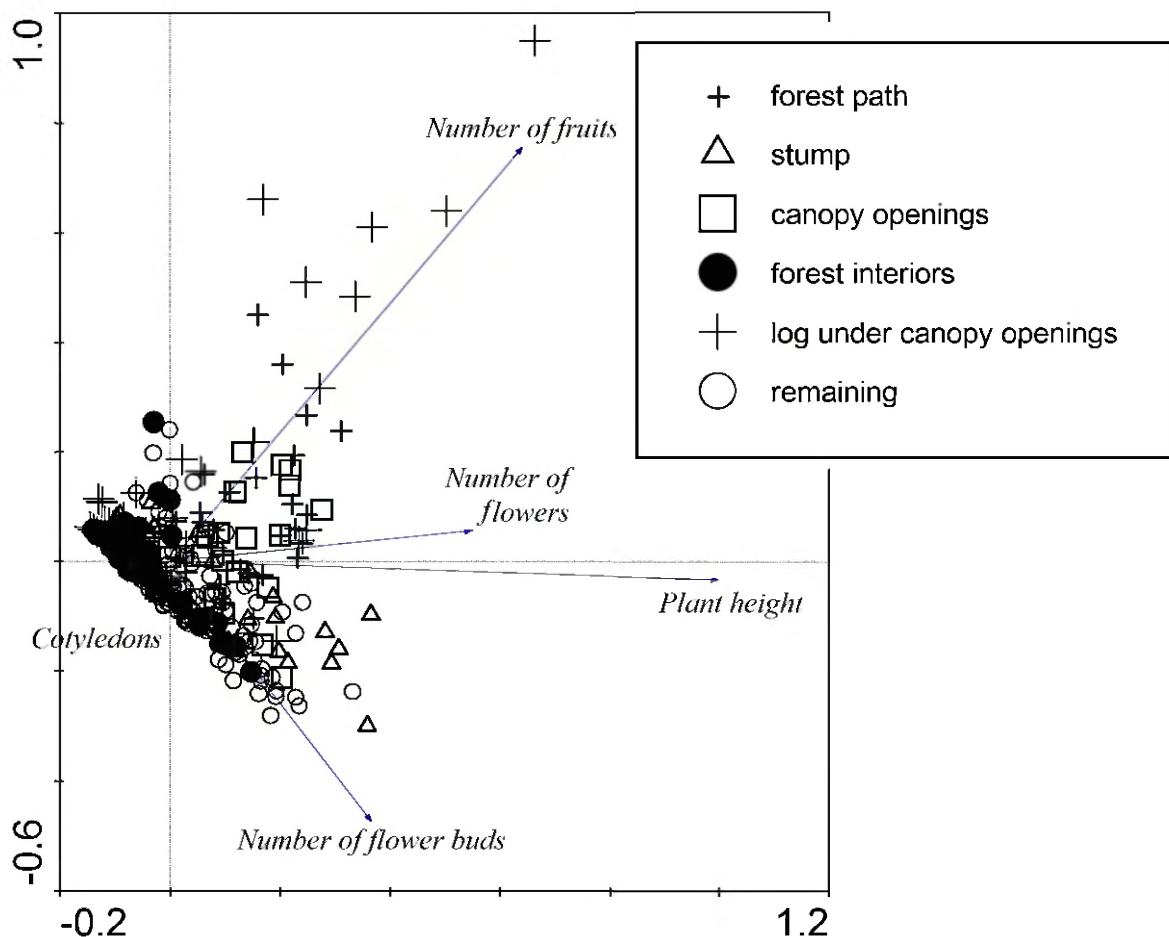

Fig. 23. Arrangement of individuals of *I. parviflora* along the two axes of the Principal Components Analysis on the basis of the selected morphometric traits and the chosen types of microhabitats

The variation within particular microhabitats is quite large when compared to the other types. Plants that are growing in logs under canopy openings; forest paths; canopy openings and stumps are highly variable. The plant traits that differentiated individuals of *I. parviflora* the most were the height of a plant and the number of flower buds (Tab. 11). The number of flowers correlated with the size of a plant (Fig. 23).

Tab. 11. The component loadings of particular plant traits

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5
Proportion of Variance	0.419	0.217	0.189	0.128	0.047
Cumulative Proportion	0.419	0.636	0.825	0.953	1.000
number of flowers	-0.509	0.124	-0.097	**0.806**	-0.257
number of fruits	-0.523	0.262	-0.311	-0.565	-0.492
number of flower buds	-0.244	**-0.744**	0.505	-0.092	-0.352
cotyledons	0.090	-0.591	**-0.799**	0.060	0.026
stem height	**-0.632**	-0.113	0.027	-0.138	**0.753**

The plants differ in mean values among the microhabitats that had been distinguished, which is shown in Table 12. The tallest individuals were found under canopy openings, on treefall disturbances and forest paths, whereas the smallest plants in terms of the height of stem grew on dead logs under a canopy of trees (Tab. 12). The highest number of flower buds was reported for plants that were growing in a canopy opening, on treefall disturbances and in areas near dead logs. Plants that were growing in forest interiors, dead logs and stumps had a lower number of flower buds on average.

Tab. 12. Comparison of plant traits (Mean±SD) among the selected types of habitats. Different letter near values in a column indicate significant differences in the medians (Kruskal-Wallis test followed by Conover test)

n	Habitat	Height of stem	Number of flower buds		Number of flowers		Number of fruits		Presence of cotyledons %
65	Forest interior	13.9±10.0 fg	0.8±1.3	c	0.3±0.5	efg	0.6±1.6	ef	16.9
50	Canopy opening	32.7±15.5 a	3.2±4.3	a	1.8±3.2	ab	2.7±3.9	bc	12.0
60	Area near log	24.9±13.0 bc	2.5±2.0	a	0.6±1.6	ef	0.2±0.6	fg	1.7
20	Log under canopy	10.9±4.8 g	0.8±1.2	c	0.1±0.2	g	0.1±0.2	fg	0.0
50	Log under canopy opening	23.9±26.1 ef	0.1±0.2	d	1.5±2.8	cd	5.8±10.6	b	0.0
50	Root plate	14.5±7.0 fg	1.3±1.3	bc	0.5±0.6	de	0.1±0.1	g	4.0
50	Treefall disturbance	30.7±12.9 a	2.9±2.8	a	1.5±1.1	a	2.3±2.4	b	4.0
30	Hollow	20.6±12.2 cde	1.0±1.7	bc	0.5±0.6	de	0.8±1.4	de	33.3
50	Path	32.9±17.4 ab	1.8±2.4	b	1.6±1.5	a	5.1±5.1	a	0.0
50	Root collar	18.8±8.4 de	1.1±1.3	bc	0.2±0.4	fg	0.1±0.5	fg	10.0
40	Stump	28.8±21.9 cd	0.9±1.3	c	3.2±6.2	bc	1.21.8	cd	0.0

The pattern for the number of flower per plant is not congruent with previous results. Generally, the number of flowers was lower in all types of microhabitats. The highest was observed in stumps but with a high degree of variation (Tab. 12). Other microhabitats with the highest number of flowers in *I. parviflora* were: canopy openings, forest paths and dead logs under canopy openings. The plants with a large number of flowers per plant were the least abundant in dead logs under canopies, in forest interiors and on root collars (Tab. 12).

The plants with the highest number of fruits per plant occurred on the forest paths followed by on treefall disturbances, dead logs under canopy openings, whereas plants with the lowest number of fruits were recorded in such microhabitats as dead logs under canopy openings, on root collars and areas near dead logs (Tab. 12).

The habitats also differed in relation to the presence of cotyledons in plants ($\chi^2 = 58$, $p<0.0001$). The highest percentage was observed in individuals that were growing in hollows followed by those that were growing in forest interiors, under canopy openings and on root collars (Tab. 12).

The tallest plants were associated with well-lit sites such as paths, treefall disturbances and canopy openings. It is already known that *I. parviflora* grows better and in large masses in such places (Coombe 1956; Trepl 1984; Eliaś 1999). A recent study by Nowińska (2010) showed that small balsam, even when it is equally frequent under canopies and gaps in forests, scores a higher cover under gaps. It is not surprising that individuals that occur under canopies and on soil were relatively small. The plants that were growing on substratums other than soil, i.e. bark or decaying wood, were strange and atypical. Some of them such as those that were growing on stumps and on dead logs but with good light conditions were taller than plants in forest interiors. The latter still had at least one cotyledon. Only plants that were growing in hollows in trees had cotyledons more frequently. A comparison of plants from various microhabitats suggests that the specimens also differed in phenology. In the literature there are some reports of the colonization of dead wood by small balsam (Piskorz, Klimko 2001; Chmura 2008c; Nowińska *et al.* 2009; Staniaszek-Kik, Żarnowiec 2013). Previous studies analyzed the density and height of plants on various microsites in the vicinity of uprooted hornbeam *Carpinus betulus* and spruce *Picea abies* trees.

In the nature reserves of the Wielkopolski National Park, the mean height of plants that were found on dead logs was between ca. 20-55 cm and the tallest individuals reached ca. 90 cm (Piskorz and Klimko 2001). Thus, they were markedly taller than the specimens of *I. parviflora* that were observed on fallen beech trees in the present study. Piskorz and Klimko (2001) also gave the heights of other plants that occurred in the remaining structures near

treefalls. The plants in that study were of similar sizes as the individuals in the present study (between 20 cm-55 cm). It is possible that plants that were growing on fallen trees were measured close to root plate of uprooted trees in the Wielkopolski National Park. The authors wrote about sections of fallen trees from both the side of the trunk or root collar and at a farther distance from the root plate and these areas are sometimes covered by remnants of soil. When the amount of soil is quite large, it forms suitable conditions for plants to develop.

A Redundancy Analysis RDA (Fig. 24) of plant traits of *Impatiens parviflora* from the microhabitats that were studied and the environmental variables showed that light availability followed by ratio of nitrogen and carbon are the most important explanatory factors. Other important significant variables are the content of magnesium, sodium, calcium and phosphorus (Tab. 13). The light influences the height of plants and the number of flowers per plant and indirectly and more weakly the number of fruits. The morphometric variables such as the presence of cotyledons and the number of flower buds do not seem to be strongly affected by abiotic variables.
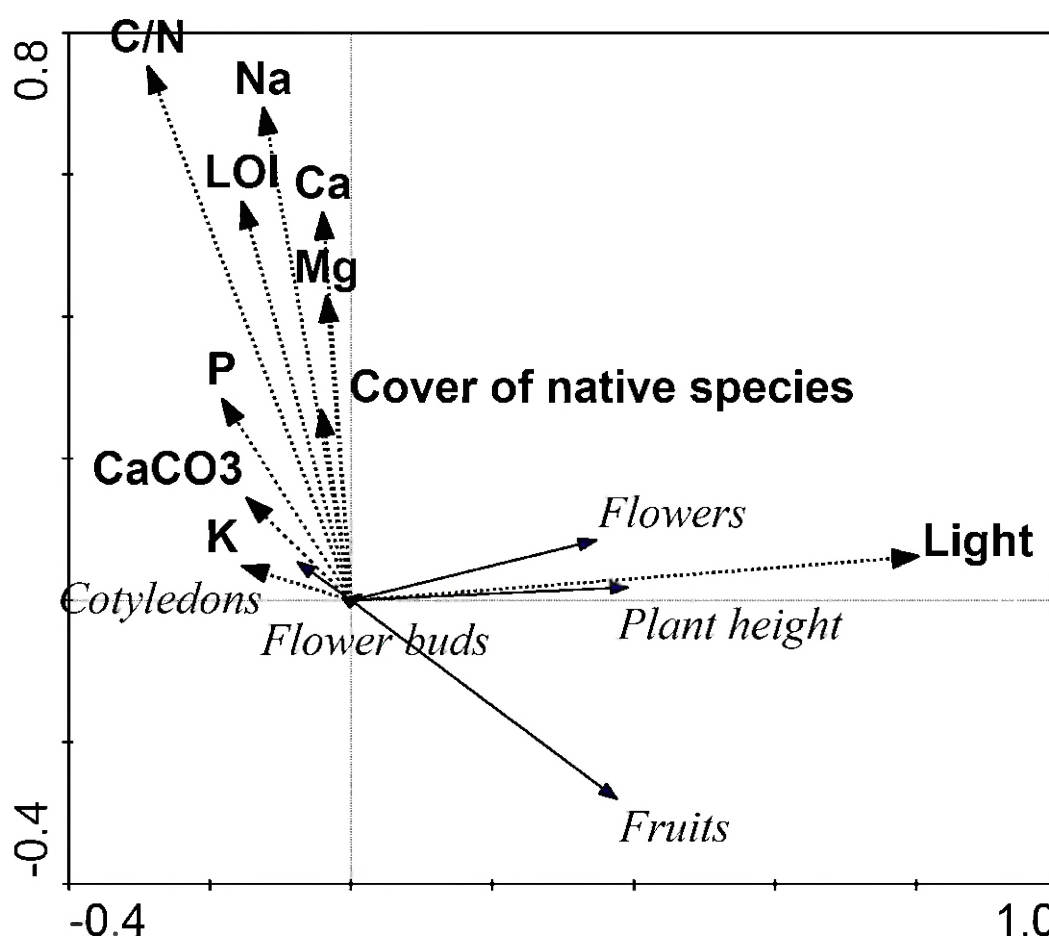

Fig. 24. Relations between plant traits and selected environmental variables based on RDA

Tab. 13. Summary of the Monte Carlo test of RDA based on the morphometric traits of *I. parviflora* and selected environmental variables

Variable	P	F
Light	0.001	52.96
C/N	0.010	5.92
Ca	ns	2.69
CaCO$_3$	0.037	4.27
LOI	ns	1.16
Mg	0.006	8.75
Na	0.008	7.21
P	0.042	3.37
Total cover of native species	ns	0.39
K	ns	0.70

This analysis also confirmed the well-recognized fact that light conditions (Coombe 1956; Trepl 1984) are the most important factor for the growth of small balsam. It has an impact on all of the parameters except the presence of cotyledons (Fig. 24). What is interesting is that the content of nutrients is correlated with the cover of native plants, which suggests that in these microhabitats nutrients mainly influence native species and small balsam is not as dependent and has low biotopic requirements.

Temporal changes in habitat occupancy and association with plant traits

Taking into account changes over the course of time and variations among the microhabitats, statistical analyses revealed many significant differences. Seedlings of *I. parviflora* that were growing in various microhabitats differed in survival during the time of the study (G=297.8, df=40, p<0.0001). From mid-April until mid-May, 100% of the seedlings in dead logs under canopy openings, on root plates, treefall disturbances and on root collars and stumps survived. During the last time series, i.e. in the second half of September, 70% and 60% in canopy openings on soil and forest paths survived, respectively. No plants were recorded in habitats such as dead logs under canopies, treefall disturbances and hollows (Fig. 25) in the last time series. The mean survival percentage of seedlings of *I. parviflora* was ranked as follows: forest paths (88.4%), area near dead logs (88.0%), canopy openings (86.0%), forest interiors (82.6%), root plates (71%), hollows (68.6%), root collars (60.8%), stumps (65%), logs under canopy openings (53.1%), treefall disturbances (38.6%) and logs under canopies (32.5%).

The mean number of cotyledons also differed among the habitats (Kruskal-Wallis, χ^2= 30.75, df = 10, p< = 0.001) and among the time series (Kruskal-Wallis χ^2= 529.47, df = 5, p<

= 0.001). In the second half of April, all of the plants had two cotyledons except for those on forest paths where single individuals with one cotyledon were found but these did not survive until the next time series (Fig. 26). The mean number of cotyledons was estimated at up to two until the second half of May in the following microhabitats: forest interiors, canopy openings, areas near logs, root plates, treefall disturbances, hollows and root collars. In the remaining microhabitats there were single plants that had only one cotyledon, thus the mean values were more than 1.5 cotyledons per plant. In forest interiors, canopy openings and hollows, no individuals with at least one cotyledon were observed in the second half of June; however, in the remaining microhabitats, plants with cotyledons were still observed. Individuals with one cotyledon were noted along forest paths until the second half of July.

The seedling height varied greatly during the time of the study and among the habitats (Tab. 14). Significant differences occurred in each of the time series among microhabitats (Tab. 15).

In the second half of April seedlings of *I. parviflora* were tallest along forest paths and in areas near dead logs and on average reached 5.9 and 4.3 cm, respectively. In mid-May the tallest plants were found on dead logs that were growing under canopies – ca. 12 cm, followed by plants that were growing near tree root collars, treefall disturbances, hollows and stumps (Fig. 27). In mid-June the tallest plants of small balsam were observed in hollows (ca. 27 cm), on root collars and in canopy openings. Because some seedlings died, the mean height of individuals on dead logs under canopies decreased to ca. 6 cm – the lowest value that was recorded among the microhabitats that had been distinguished (Fig. 27). The tallest plants on stumps were observed in July, August and September and reached 39-45 cm. From mid-August until September a significant increase in the mean height of plants was noted for forest interiors and canopy openings which finally reached ca. 34 cm (Fig. 27). There were no significant differences in the mean height of plants among the microhabitats in September (Tab. 15).

The number of leaves that were related time and the variations among microhabitats showed a trend that was similar to that of the mean height of plants (Fig. 28). Differences among microhabitats were noted for the second (the second half of May) and third time series (the second half of June). The first leaves were only observed in May. The mean number of leaves per plant, from the highest to the lowest, is ranked as follows: stumps (11.3), hollows (10.6), root collars (8.7), areas near logs (7.6), forest paths (7.2), root plates (6.1), forest interiors and canopy openings (5.8), logs under canopy openings (5.7), treefall disturbances (5.0) and logs under canopies (4.9).

The first flower buds in individuals of *I. parviflora* only appeared in mid-June. In July plants differed significantly in the mean number of flower buds among the microhabitats (Tab. 14-15). The highest number was observed on plants that were growing on stumps and the lowest on plants in treefall disturbances (Fig. 29) during this period. In August plants in hollows had the highest mean number of flower buds. The mean number of flower buds decreased in all of the habitats in September.

The mean number of flowers per plant differed significantly only in June when the first flowers developed (Tab. 14-15). Generally, the number of flowers was not high in any of the microhabitats during the time of the study. The highest was noted for plants that were growing in stumps and hollows (Fig. 30).

Single fruits on plants were observed for the first time in June (Fig. 31). The plants that were growing near root collars, stumps and on root plates had a significantly higher number of fruits (Tab. 14-15, Fig. 31) in comparison with the other types of microhabitats. Individuals of small balsam that were growing in treefall disturbances or on dead logs under canopies developed fruits singly and only in July. These plants usually died out faster than in the other types of microhabitats.

Similar plant history traits were analyzed in temporal and spatial research. The height of adult plants was a factor for spatial variation, whereas for changes in time, the height of seedlings was analyzed until their death. The number of leaves was considered to be important as well as the mean number of cotyledons, which obviously varies from zero to two, when examining the development of individuals. Only the presence of cotyledons was important for the spatial research. The above-mentioned life history traits such as plant height, the number of flowers and fruits are studied very often. The first one is a measure of the gregariousness of plants and the next two indirectly indicate reproductive potential. The changes in density that were observed were similar to those that were demonstrated by Kujawa-Pawlaczyk (1991) with a peak in the abundance of plants in June and July; however, due to method that was applied, individuals that emerged later were not included in the observations.

The highest seedling mortality on dead logs or stumps without a layer of normally developed soil is determined by unfavorable abiotic conditions. It was shown that the mortality of seedlings for the native congener *I. noli-tangere* is caused by moisture and light conditions and its neighbors (Falińska 2004). In the present study the lack of moisture appeared to be the most crucial factor. The exceptions were plants that were growing in treefall disturbances, which died out quite quickly. The highest density of plants was observed

on these sites, which could lead to higher intraspecific competition. All of the observations in relation to phenology and differences in morphometric traits were done on labeled individuals. Thus, only one cohort of plants was analyzed in the present study. The model of seasonal dynamics of one or more cohorts was elaborated on by Symonides (1988a). Germination and seedling emergence usually take place in a short time and the development of particular stages of the life cycle run almost simultaneously. Obviously, differences among individuals that are derived from various microhabitats are more considerable in disturbed and nutrient-poor microcosms such as those in the present study.

The most important finding was that in almost all of the microcosms that were studied, with the exception of plants that were growing on dead logs under canopies plants developed fruits, i.e. on sites without a developed layer of soil and with poor light conditions. High fecundity is a typical attribute for annual plants and is also the optimal model of actual strategy. Seeding fruits is the only chance to survive and therefore it is obvious that plants allocate biomass to the generative organs even under unfavorable conditions (Symonides 1988b).

Other important features that were not investigated in the present study are: self-pollination, which was quite well-recognized by Vervoort *et al.* (2011) and Piskorz (2005), who studied the presence of cleistogamous flowers. Symonides (1988b) believes that amphicarpy in annuals, i.e. the presence of both cleistogamous and chasmogamous flowers, gives them an evolutionary advantage, especially in disturbed habitats.

Tab. 14. Effect of habitat and the time of measurement on the morphometric features of *Impatiens parviflora* seedlings (Kruskal-Wallis test)

	height of seedlings			number of leaves			number of flower buds			number of flowers			number of fruits		
	χ^2	df	P	χ^2	df	P	χ^2	df	P	χ^2	df	P	χ^2	df	P
Habitat	27.09	10	0.002516	20.0	10	0.0286	21.21	10	0.01961	28.32	10	0.001599	37.05	10	<0.0001
Time	331.53	5	<0.0001	404.88	5	<0.0001	311.73	5	<0.0001	190.40	5	<0.0001	268.89	5	<0.0001
Habitat:															
series I	67.66	10	<0.0001	-	-	-	-	-	-	-	-	-	-	-	-
series II	41.90	10	<0.0001	30.58	10	0.0006869	-	-	-	-	-	-	-	-	-
series III	46.07	10	<0.0001	22.79	10	0.01155	16.10	10	ns	37.00	10	<0.0001	-	-	-
series IV	28.62	10	0.001434	17.85	10	ns	25.28	10	0.004823	13.87	10	ns	22.51	10	0.0127
series V	30.55	9	0.0003532	15.77	9	ns	18.94	9	0.0257	14.04	9	ns	30.39	9	0.0003751
series VI	6.63	7	ns	12.50	7	ns	4.47	7	ns	5.85	7	ns	8.78	7	ns

Abbreviations: series I: 16.04.07, series II: 18.05.07, series III: 14.06.07, series IV: 17.07.07, series V: 17.08.07, series VI: 22.09.2007

Tab. 15. Result of the post-hoc Conover test. Different letters in a column indicate significant differences at p<0.05. See Table 13 and Figures nos. 27-31

	height of seedlings					number of leaves		number of flower buds		number of flowers	number of fruits	
series	1	2	3	4	5	2	3	4	5	3	4	5
Forest interior	de	g	cde	abc	de	cd	bc	abcd	abc	b	abcd	cde
Canopy opening	a	defg	a	bc	e	d	a	abcde	bc	b	de	de
Area near log	ab	cdef	bcd	a	abc	bc	abc	ab	a	b	ab	abc
Log under canopy	e	a	e	bc		a	c	cde	-	b	cde	
Log under canopy opening	de	efg	de	bc	de	ab	abc	de	c	b	bcde	cd
Root plate	e	fg	abc	a	abc	ab	a	abcd	ab	b	abc	ab
Treefall disturbance	bc	abc	bcd	bc	cde	a	c	e	abc	b	e	e
Hollow	cd	abcd	a	a	abc	ab	a	abcd	ab	a	abcd	cd
Forest Path	a	bcde	abc	ab	bcd	a	ab	abc	abc	a	abcd	ab
Root collar	cd	ab	a	a	a	abc	ab	bcde	abc	b	bcde	a
Stump	e	abcde	ab	a	ab	ab	abc	a	a	b	a	a

Abbreviations: series 1: 16.04.07, series 2: 18.05.07, series 3: 14.06.07, series 4: 17.07.07, series 5: 17.08.07, series 6: 22.09.2007
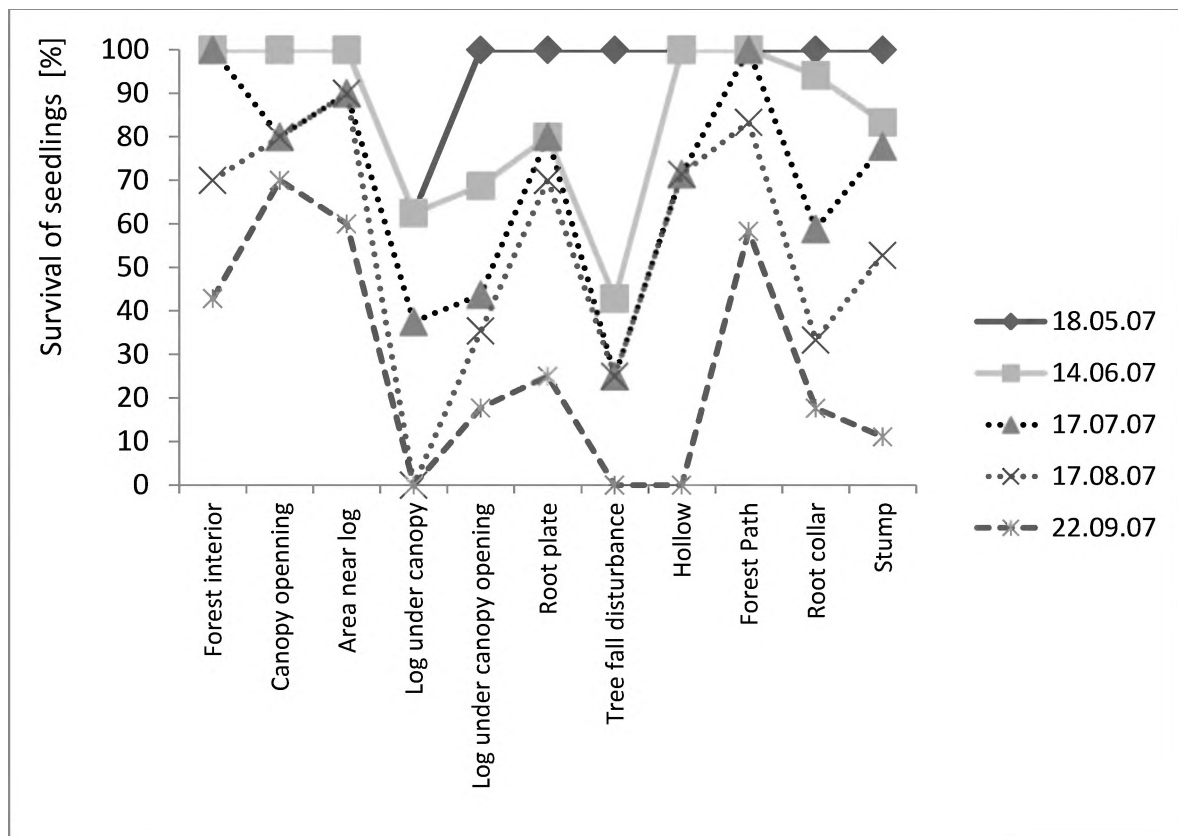
Fig. 25. Percentage of survival of *Impatiens parviflora* seedlings over time in particular microhabitats since 16.04.2007
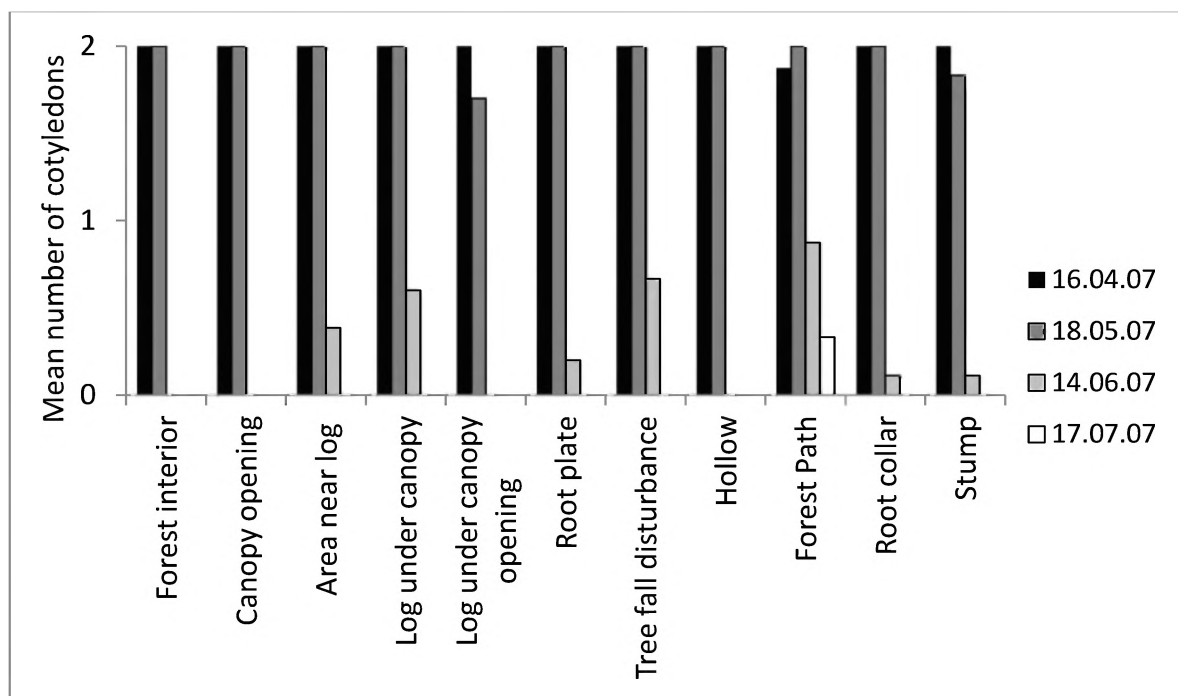
Fig. 26. Comparison of the mean number of cotyledons in particular microhabitats over time
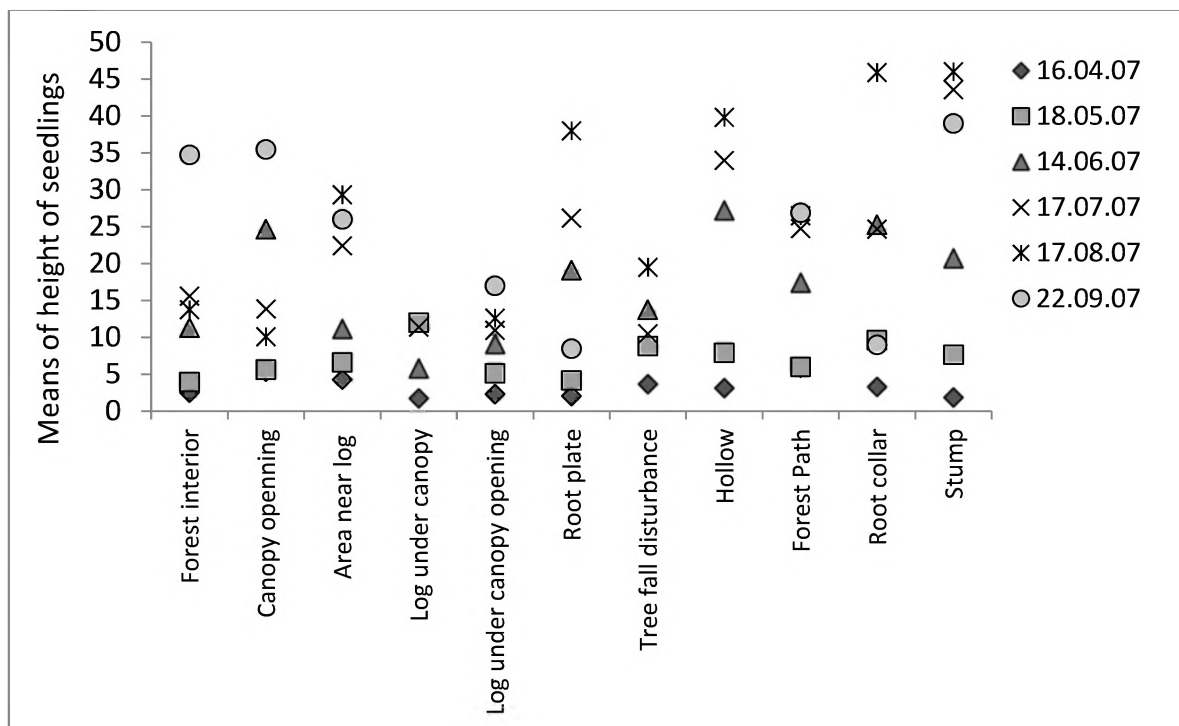
Fig. 27. Effect of time and microhabitat on the height of *Impatiens parviflora* seedlings
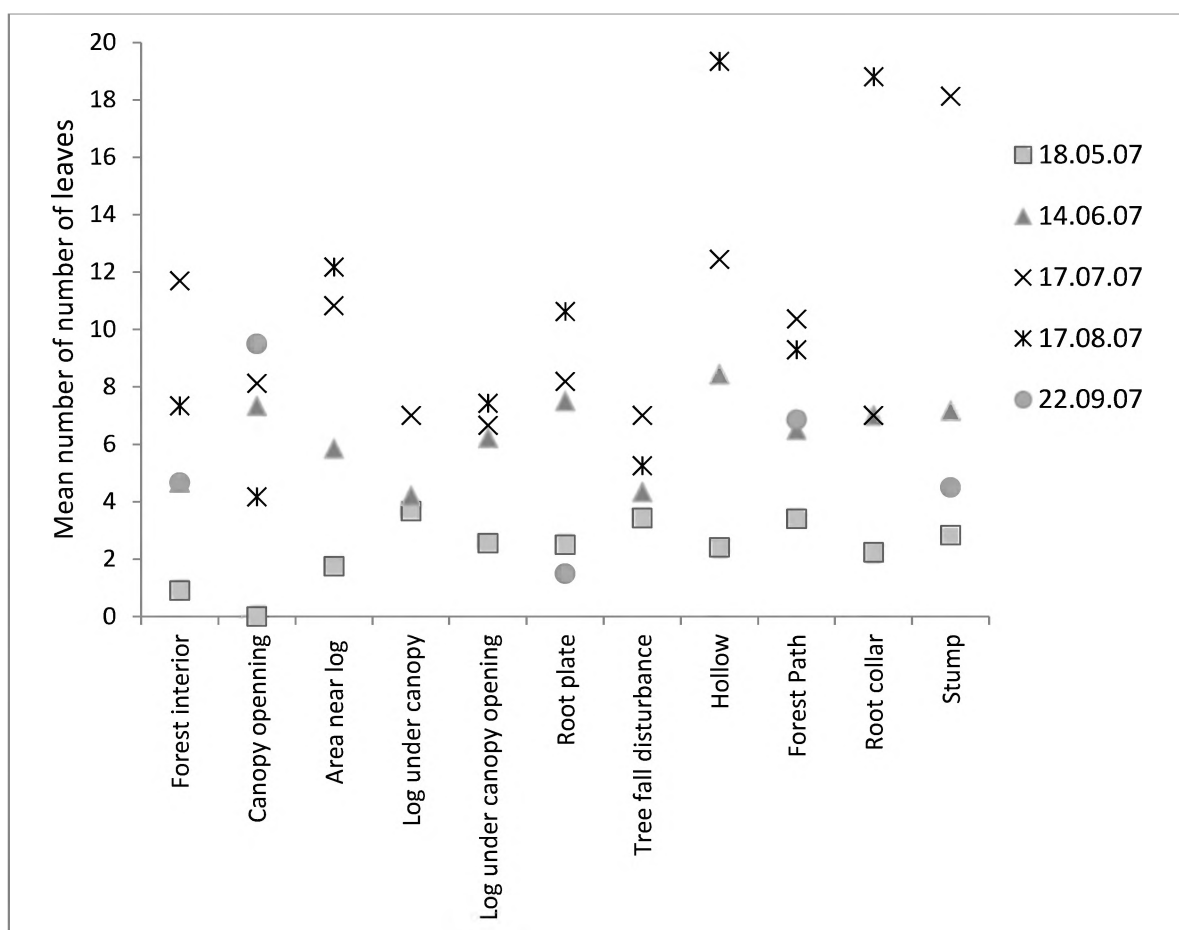
Fig. 28. Effect of time and microhabitat on the number of leaves of *Impatiens parviflora* seedlings. No leaves were recorded on 16.04.2007
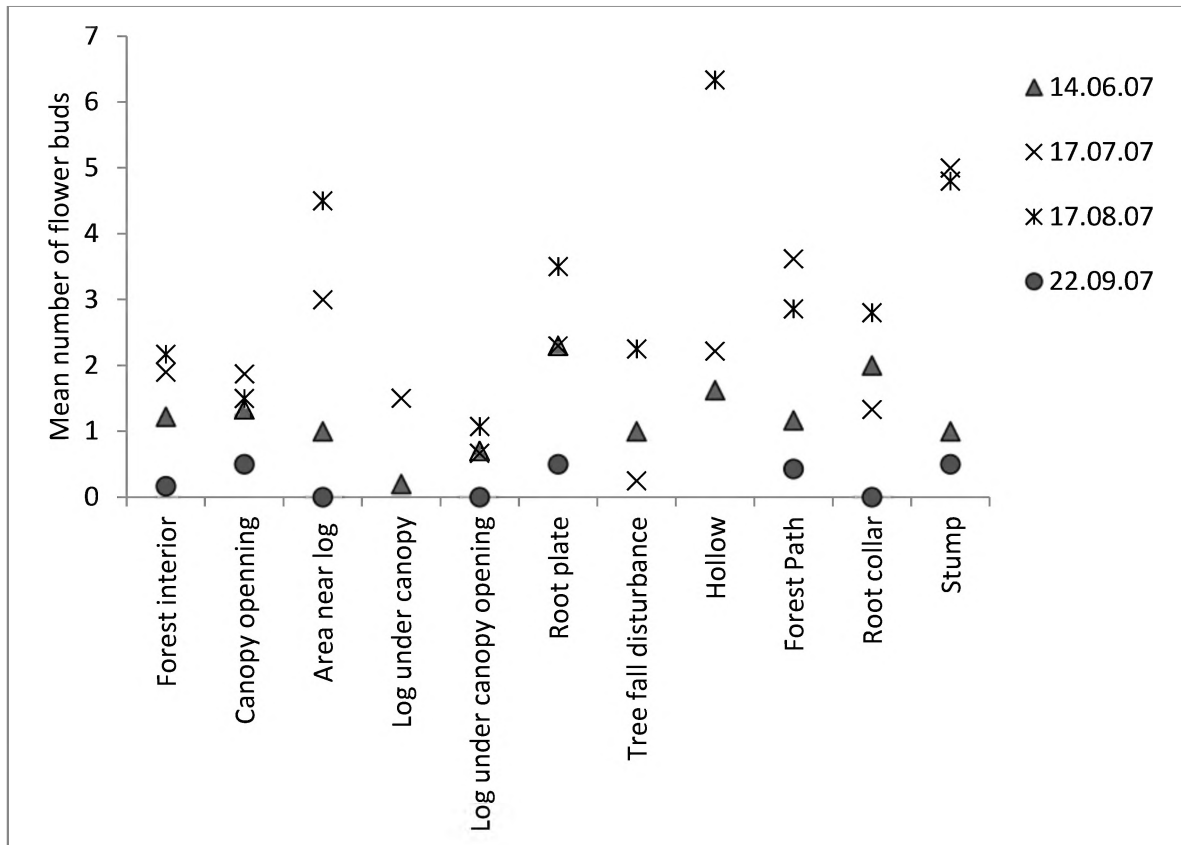
Fig. 29. Effect of time and microhabitat on the number of flower buds of *Impatiens parviflora*. No flower buds were recorded on16.04.2007 and 18.05.2007

Fig. 30. Effect of time and microhabitat on the number of flowers of *Impatiens parviflora*. No flower buds were recorded on 16.04.2007 and 18.05.2007

Fig. 31. Effect of time and microhabitat on the number of fruits of *Impatiens parviflora*

Irrespective of the type of flowers, the majority of individuals from the microhabitats that were studied survived until June and July and bore fruits. It turned out that those that had the highest reproductive potential were plants that were growing where the soil layer was available (on root collars and root plates where a remnant of soil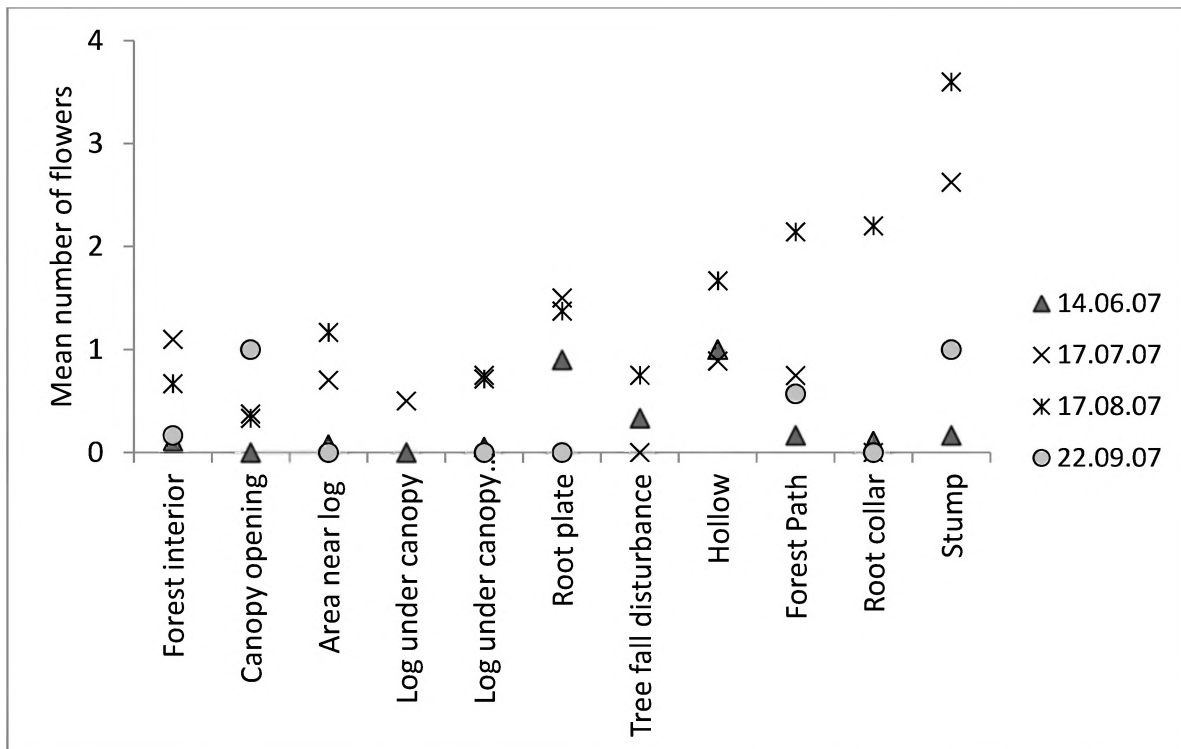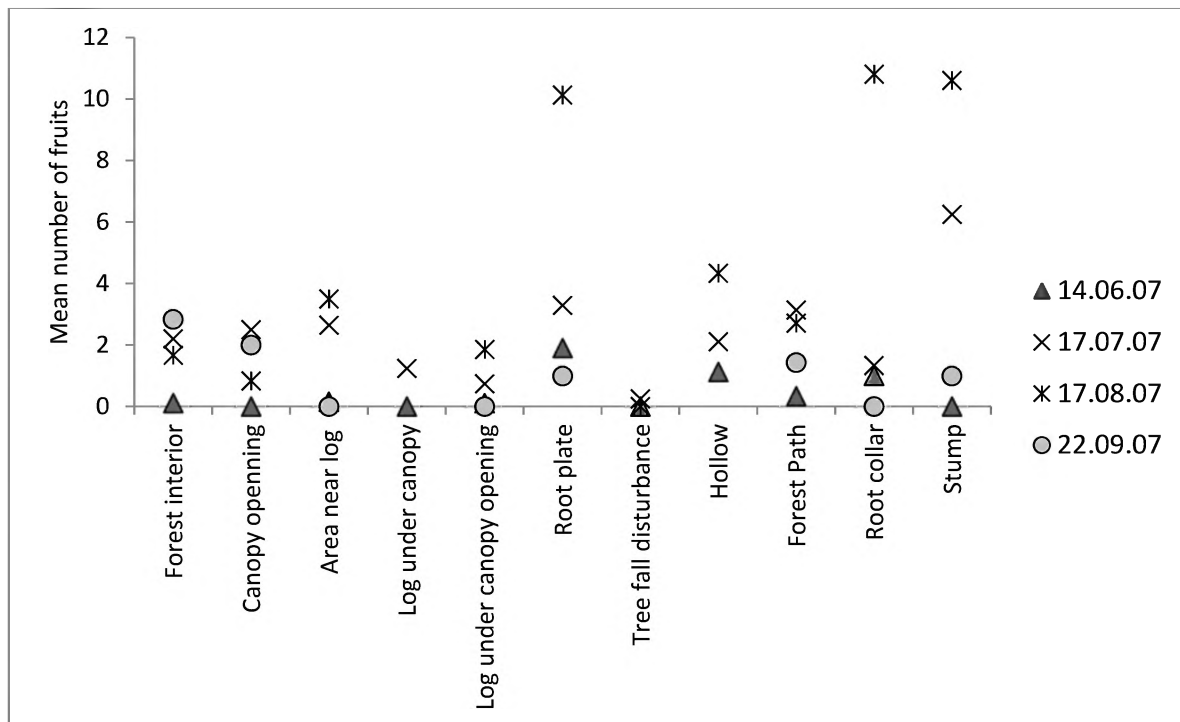 is present. The tops of stumps seem to have unsuitable conditions for *I. parviflora*. However, the structure of the wood enables them to hold moisture, which is believed to significantly increase during wood decay (Bütler *et al*. 2007). Due to numerous slits, fallen leaves and low amounts of decaying bark they can undergo decomposition as well thereby beginning the process of the formation of humus can occur, which creates quite favorable conditions for small balsam.

Impact of aspect, light and nutrients on the occurrence of species

Figure 32 shows the differences in the heights of plants of *Impatiens parviflora* on two types of slopes and in various time series. There are significant differences between southern-facing and northern-facing slopes and the time of the measurements (one-month intervals). Statistical analyses revealed significant differences in space and time (Tab. 16). A higher degree of growth and the heights of the plants were generally detected on northern-facing slopes (Fig. 32).

It has been known for some time that small balsam grows more abundantly on northern-facing slopes when compared to southern-facing slopes (Coombe 1956; Trepl 1984). Brothers and Spingarn (1992) and Small & McCarthy (2003) proved that southern-facing slopes are

characterized by a higher species richness and a lower dominance and abundance of some species. More favorable conditions, especially temperature and light conditions, create niches for more species and therefore small balsam has a smaller ecological barrier, which is manifested by the lower biocenotic resistance that it has to overcome on northern-facing slopes. Chmura (2008b) demonstrated that northern-facing slopes are overgrown by herbaceous vegetation (including *I. parviflora* and 11 other species) whose plants are taller on average. The present study shows in detail how this aspect has an impact on the height of shoots in small balsam. Possible mechanism of this phenomenon may include suppression by other plants. It was revealed that the density of individuals of *I. parviflora* affects the size of plants even in a monoculture population (Coombe 1956).
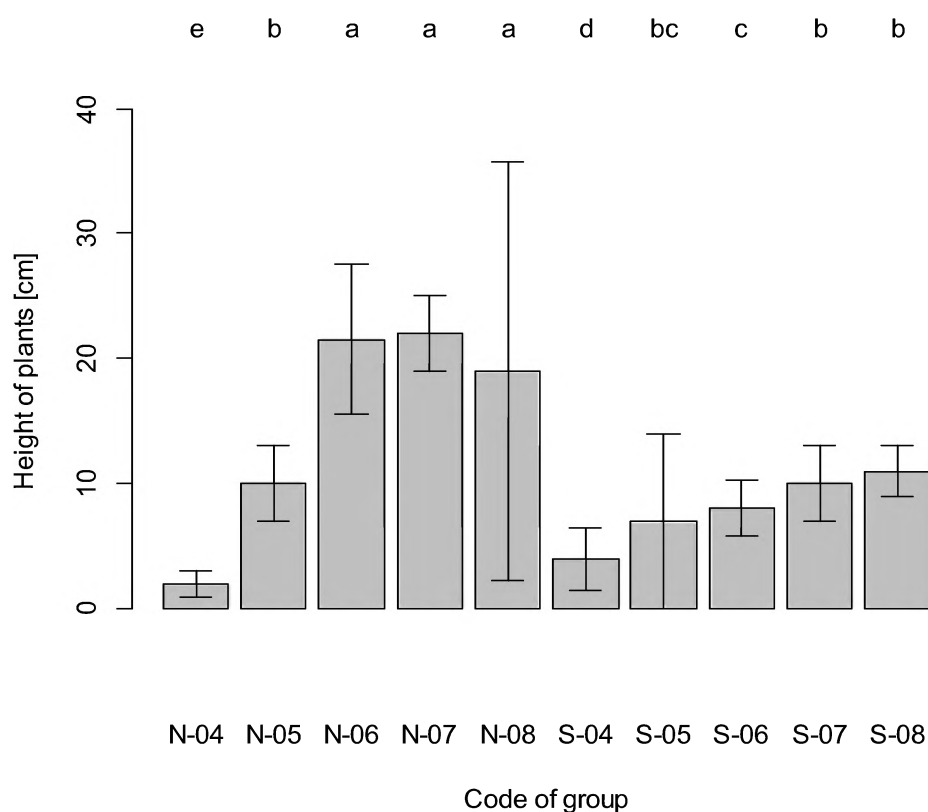
Fig. 32. The comparison of height of *Impatiens parviflora* individuals due to time and aspect. N- northern slopes, S- southern slopes, 04-08- successive months

Tab. 16. Influence of aspect and time on height of plant (Wilcoxon sum rank test and Kruskal-Wallis test)

	Statistics	P
Time	$\chi^2 = 49.5$	<0.0001
Aspect	$W = 1046$	0.03101
Time X aspect	$\chi^2 = 64.20$	<0.0001

An analysis of the presence/absence of small balsam in microhabitats that were associated with living trees (sites close to root collars and hollows), snags (root collars, hollows and the tops of broken trees) and dead log complexes (areas near dead logs, bark on logs, treefall disturbances and root plates) demonstrated significant differences in the frequency of the species (G=56.59, p<0.001).

The plants that were living in dead log complexes were present (60%) more than absent (40%) in location in which such forms and types of substratum were available. Snags, i.e. both unbroken and wind-broken dead trees, had more individuals of *Impatiens parviflora* close to their root collar than living trees (Fig. 33).

Fig. 33. Association of *Impatiens parviflora* with dead logs complex and snags in comparison with living standing trees

There is a negative medium but significant correlation between the distance from dead logs or snags and the density of *Impatiens parviflora* individuals (Fig. 34).

Fig. 34. The influence of distance from dead logs complex on density of *Impatiens parviflora* in 1m² subplots (Spearman rank correlation test)

A study by Piskorz and Klimko (2001) revealed that *Impatiens parviflora* is an efficient colonizer of microhabitats that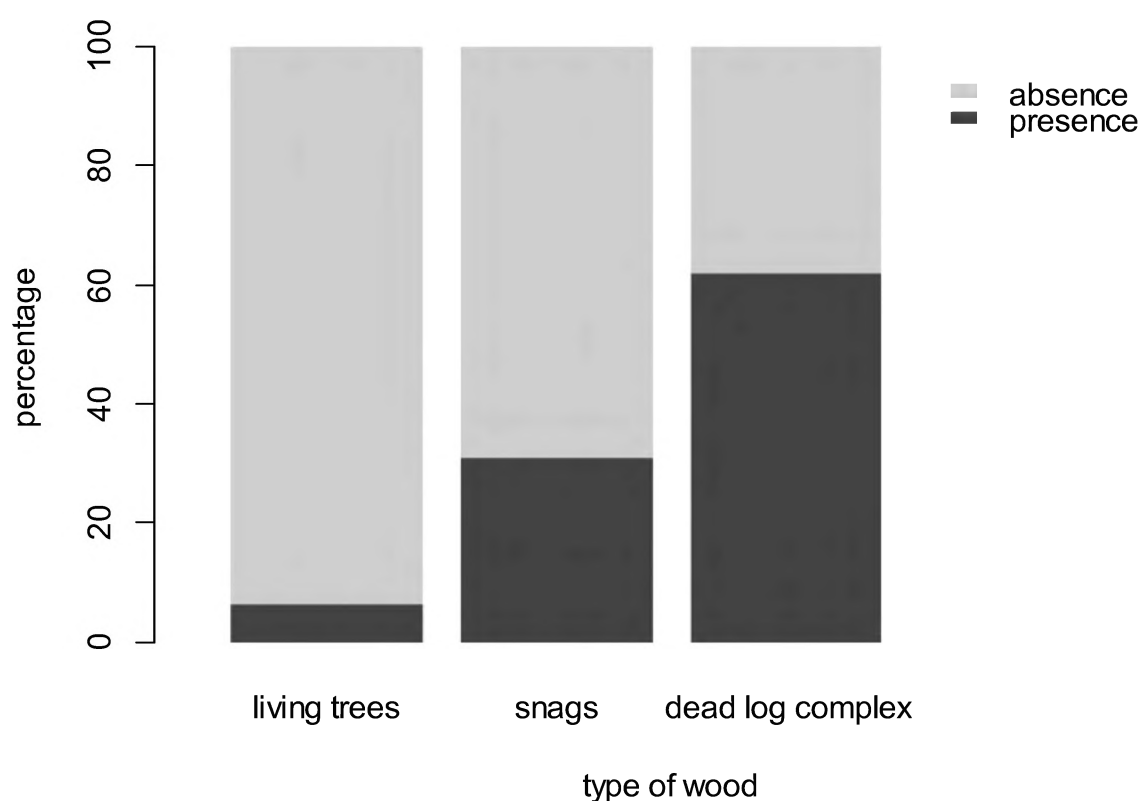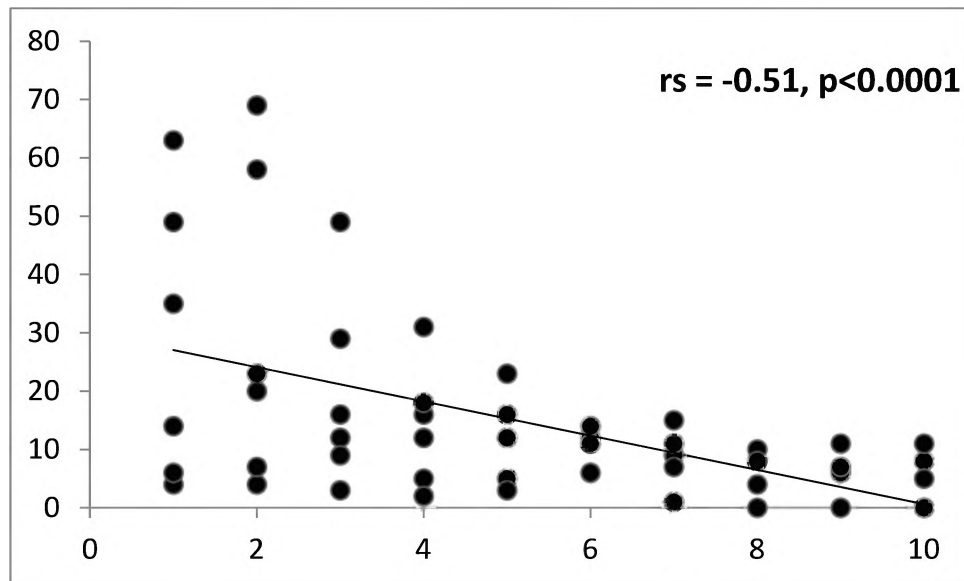 are associated with fallen dead trees. They studied fallen logs, root plates and holes in the ground. The results that were obtained are descriptive but without any statistical analyses, although they seem to be congruent with the present study. For instance, they demonstrated that with an increasing distance from the sites of tree falls the density of small balsam showed a downward trend. In both that study and the present one such differences in height can be attributed to the impact of light intensity. Some authors such as Hegi (1965), Zarzycki (1984), Zarzycki *et al.* (2002) believe that *I. parviflora* is a sciophyte. Moreover, in laboratory research, Hughes & Evans (1962) and Hughes (1965) revealed a decrease in density under full sunlight although in another lab study, Whitelam and Johnson (1980) proved that small balsam can behave like a shade-liking and open habitat species. Other authors who conducted research in the field claimed that the species is rather a photophilous species (Kujawa-Pawlaczyk 1991; Piskorz, Klimko 2001; Klimko, Piskorz 2003).

The analysis of the height of *Impatiens parviflora* plants in the four types of plots confirmed the impact of light and the presence of dead wood on their height (Tab. 17). Only the presence of dead wood does not significantly affect the size of plants. Post-hoc tests showed significant differences among individuals from the control plots (ground layer under tree canopies) and individuals from the other types of plots. There were no significant differences in the height of plants that were growing in the vicinity of dead logs under canopies (CW) and the control (C). Likewise, there were no differences between plants that were growing on plots with canopy openings (O) and plants that were growing near dead logs under canopy openings (OW) (Fig. 35).

Moreover, plants that were growing near dead logs did not differ among the plots with or without a tree canopy (CW vs. OW). The mean leaf area differed significantly between the control (C) and canopies and dead wood plots (CW) vs canopy openings (O) and plots with dead wood under canopy openings (OW) (Fig. 35), which was confirmed by the significance of the impact of light availability (Tab. 18). The individuals of the second group were characterized by a larger leaf area. The same situation concerns the biomass of leaves (Fig. 35, Tab. 18). When specific leaf area (SLA) was considered, plants from the control plots had, on average, the lowest value of this variable (Fig. 35, Tab. 19).

Tab. 17. Influence of dead wood and light availability on the height of plants (two-way ANOVA)

	Df	F	P
Canopy openings	1	45.7962	<0.0001
Dead wood	1	0.0775	ns
Canopy openings x dead wood	1	14.9858	0.000163
Residuals	146		

Table 20 presents the differences in the mean content of chemical elements that are responsible for the trophy of soils. There was a significantly lower concentration of potassium in the control and the plots with canopy opening as well as those with dead wood under canopy openings (Tab. 20). A significantly higher content of phosphorus was observed in both types of dead wood plots. There were no significant differences with respect to the concentration of magnesium due to high degree of variation within the study plots (Tab. 20). The concentration of total nitrogen was similar in all of the plots that had been distinguished (Tab. 20).

Tab. 18. The influence of presence of dead wood and canopy openings on leaf area (LA) and leaf biomass (LB) (two-way ANOVA)

	LA			LB		
	df	F	P	df	F	P
Canopy openings	1	78.712	<0.0001	1	54.8198	<0.0001
Dead wood	1	0.4075	ns	1	3.7968	0.05525(ns)
Canopy openings x dead wood	1	0.0598	ns	1	0.1772	ns
Residuals	72			72		
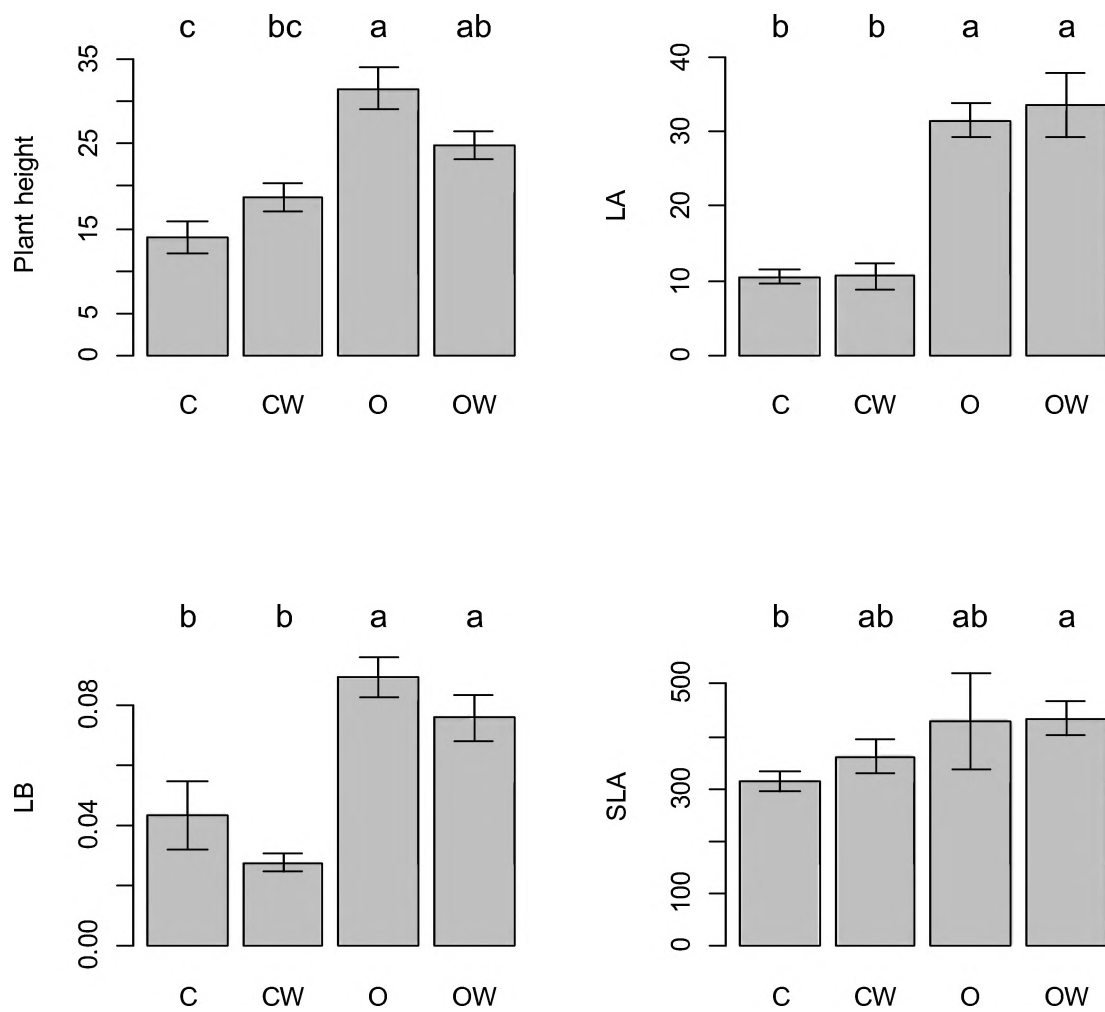
Fig. 35. Comparison of plant height (cm), leaf area LA (cm^2), specific leaf area (SLA), leaf biomass LB (g). between the types of plots. Abbreviations: C – canopy, CW – canopy and dead wood, O – openings OW – openings and dead wood present

Tab. 19. The influence of the presence of dead wood and canopy openings on specific leaf area (SLA). (Wilcoxon sum rank test and Kruskal-Wallis test)

Variable	statistics	P
Opening	W=542	0.06(ns)
Wood	W=485	0.025
Opening x Wood	χ^2= 8.48	0.036

Tab. 20. Comparison of chosen physical-chemical parameters of soils between the types of plots that had been distinguished (Kruskal-Wallis test followed by Conover test). The same letter or no letters in a column mean non-significance of differences at p<0.05

	K	P	Mg	Nt
Canopy and dead wood	34.4±48.8 a	20.7±37.0 a	30.2±59.4	0.3±0.1
Control	9.9±5.4 b	5.2±6.4 b	10.8±11.5	0.5±0.4
Canopy openings	9.6±2.6 b	7.5±5.0 b	13.6±12.0	0.3±0.2
Openings and dead wood	14.0±10.5 b	11.7±16.3 a	15.0±19.8	0.3±0.1

The results of the analysis of height among the four habitats that had been distinguished are in partial agreement with a greenhouse experiment by Elemans (2004), who proved that with a 66% level of full light and the highest level of nutrients equivalent to 300 kg N ha^{-1} per year, plants had the highest biomass that reached 10 g of the total biomass per plant. If it is assumed that the height of individuals of *Impatiens parviflora* is correlated with its biomass then the results of this study show a similar trend. Plants on plots with canopy openings were the tallest but not significantly taller than those from plots with canopy openings with dead wood. Under natural conditions the highest light intensities are at sites where the falls of trees have caused canopy gaps. As a result, plants that were growing near dead logs under canopies were taller than those that were growing on mineral soil under canopies. Thus, the trend is similar to the result of Elemans (2004) who showed that the total biomass of plants was higher at a high dose of nutrients and was at 2% when compared to low dose of nutrients with the same amount of light.

No significant interaction of light and the fertility of a habitat for SLA was observed, although the highest value was recorded for sites under canopy openings (O) and near dead logs (CW, OW) (Fig. 35). This is in contrast with Elemans (2004) who revealed the highest value of SLA for a high-nutrient treatment and 2% of light. However, SLA on sites near dead logs was higher than on sites on mineral soil under canopies. It is known that plants are capable of changing their biomass allocation as well as their leaf morphology during growth, i.e. leaf weight, specific leaf area, etc. At low light intensities plant usually allocate more biomass to the leaves and then SLA increases, whereas when the amount of nutrients is low, biomass is allocated to the root system (Poorter *et al.* 2011), although SLA can sometimes increase during nitrogen fertilization (Wang *et al.* 2012).

The discrepancy between the findings obtained in this study and the works by Peace and Grubb (1982) and Elemans (2004) result from the research design and growing conditions. In the previous work, the experiment was performed in controlled environment cabinets, whereas in the latter one the conditions were less controlled, i.e. in greenhouses. Moreover, light and nutrients

were not controlled in the present study. Differences in light and nutrients are vague because they are supposed to reflect the natural conditions in forest ecosystems. The most controversial aspect is the presence of allegedly higher levels of nutrients that can be released from decaying wood. However, higher values of potassium and phosphorus were found near dead logs in the present study. Bütler *et al.* (2007), when studying the decomposition of *Picea abies*, reported higher values of carbon and nitrogen under dead logs. In spite of the recognized knowledge that coarse wood debris contributes to nutrient cycling, little is known about this phenomenon. One more noteworthy point is that plants that grow near dead decaying logs are partially shaded and moisture conditions are certainly better.

3.3. Contribution of *Impatiens parviflora* to plant communities and biotic relations

3.3.1. The occurrence in plant communities

Phytocenological spectrum

Small balsam is encountered in many types of forest communities, which is shown in the synoptic table (Appendix 1). Not all vegetation units can be classified into a particular plant association within the Braun-Blanquet system. Despite some difficulties in the classification of plant communities in which the species is present, it has been demonstrated that *Impatiens parviflora* tends to be confined to deciduous or mixed deciduous forests. An analysis of species that accompany small balsam in regard to their syntaxonomical affinity showed that the cover abundance of *I. parviflora* is positively correlated with the cover of representatives of broad-leaved deciduous forests (Tab. 21). The species that represent coniferous and mixed coniferous forests (*Vaccinio-Piceetea*) negatively correlated with the cover of small balsam. There was also a negative but weaker correlation with representatives of swamp riparian alder forests (*Alnetea glutinosae*). No significant correlation was found with species of acidophilous oak forests (Tab. 21).

Tab. 21. Spearman rank correlation coefficients between the cover of representatives of particular classes of forest vegetation and the cover of *I. parviflora*

class	Rs	P
Querco-Fagetea	0.37	<0.0001
Vacccinio-Piceetea	-0.28	<0.0001
Alnetea glutinosae	-0.13	0.0041
Quercetea robori-petraeae	-0.07	ns

During phytosociological research that was conducted in the Silesian Upland, 12 vegetation units that had been distinguished in forest areas were recorded (Appendix 1). Among the 485 phytosociological relevés where neophyte species were present, small balsam occurred in 131.

Impatiens parviflora was the most frequent in the community named after its abundant occurrence – *Pinus sylvestris – Impatiens parviflora*, where the median cover was estimated at 63% (Appendix 1). It is a secondary and ephemeral forest community that formed after the removal of shrubs and digging of soils and it was encountered 11 times. Other forest communities in which the species was found are given in a descending order in terms of their frequency: *Ficario-Ulmetum* (75% of relevés), *Fraxino-Alnetum* (71%), beechwoods of the *Fagenion* alliance (6.4%), oak-hornbeam forests *Tilio-Carpinetum* (60.6%), swamp alder forests *Ribeso nigri-Alnetum* (60%), acidophilous beechwood *Luzulo pilosae Fagetum* (58.3%), acidophilous oak forests *Calamagrostio-Quercetum* (41.9%), mixed coniferous forests *Querco roboris-Pinetum* (41.4%), forest communities of *Querco-Fagetea* class (35.3%), *Molinio-Pinetum* (25%), *Calamagrostio villoase-Pinetum* (25%) and *Leucobryo-Pinetum* (12.5%).

The median cover of *I. parviflora* was not very high. Its median cover only exceeded 10% in deciduous forests: oak hornbeam forests, mixed coniferous forests and swamp alder forests. Its cover on average amounted to 7% in disturbed anthropogenic communities of *Querco-Fagetea* while in the remaining types of forest communities, the species cover of small balsam varied between 2-3% (Appendix 1).

The results that were obtained show a phytosociological amplitude that is typical for small balsam. Since Ćwikliński (1978) and (Trepl 1984), it has been known that the species occurs in many types of plant associations, especially in broad-leaved deciduous forests. However, during the collection of the standard phytosociological research, some sites that do not fully fit into the known phytosociological units – syntaxon at the rank of plant association are omitted, which was pointed out and criticized by Holeksa and Woźniak (2005). Nevertheless, Cabała (1990) while studying the forest vegetation in the Silesian Upland and collecting around 2000 phytosociological relevés revealed the presence of small balsam in communities of *Querco roboris-Pinetum, Calamagrostio-Quercetum petraeae, Ficario-Ulmetum campestris, Carici remotae-Fraxinetum, Tilio-Carpinetum, Luzulo pilosae-Fagetum* as well as in a community of *Eu-Fagion, Dentario glanduloase-Fagetum*. The species was especially abundant and frequently represented in oak-hornbeam forests. Small balsam is rare and not abundant in the remaining forest communities, which could be the result of the selection of the sites for collecting phytosociological records, *a priori* the special selection of relevés for synoptic tables, or it could reflect the state of the invasion level of *I. parviflora* in the late 1980s.

Irrespective of classification of the forest communities within the Braun-Blanquet approach, the analysis of the relationships between the cover abundance of *I. parviflora* and representatives of particular phytosociological classes showed a distinct fidelity of the species to deciduous vegetation. A median and weaker negative relationship with representatives of coniferous forests and bog forests, respectively, is also relevant. It usually has a positive relationship with representatives of acidophilous oak forests; however, in this case the relationship is slightly negative and non-significant, which may result in fewer syngenetic species of *Quercetea robori-petraeae*, which could bias the statistical analyses.

The occurrence of species against the background of invasion level in plant communities

In addition to small balsam, 16 other invasive alien species were found (Appendix 1). The most frequent were: *Quercus rubra, Padus serotina, Solidago gigantea* and *S. canadensis*. Among the 13 vegetation units that had been invaded, some phytocoenoses were characterized by a relatively large contribution of neophytes. Taking into account the ratio of cover of all of the neophytes to the cover of all of the species that were present D_N, the most invaded forest communities were: *Pinus sylvestris – Impatiens parviflora* ca. 88%, beechwoods (communities of the *Fagenion* alliance) and floodplain forests (*Ficario-Ulmetum* 70% and *Fraxino-Alnetum* 63%), while those that had an intermediate degree of invasion were swamp alder forests *Ribeso nigri-Alnetum*, oak-hornbeam forests and acidophilous beech forests *Luzulo pilosae Fagetum* (Fig. 36). The forest community with the lowest abundance of neophytes was a pine forest *Leucobryo-Pinetum* 3.8%.

The participation of *I. parviflora* in the invasion of forest communities is rather high. The mean P_N is 10.6. The value of P_N among the forest communities varied between 2.3% for *Molinio-Pinetum* and 36.9% for a *Pinus sylvestris* community (Fig 37). For comparison, the P_N of *Padus serotina* and *Quercus rubra* were only 0.18 and 0.23, respectively.

The number of alien species that can be found in forests depends on their source. Chmura (2004) listed 40 species that occur in forest areas in this region, whereas Tokarska-Guzik, *et al.* (2007) mentioned nine species among the 45 that they found in the area. According to her and collaborators in the research on the Silesian Upland, *I. parviflora* prefers deciduous forests on more fertile and humid soils, while the other most frequent species, *Quercus rubra* and *Padus serotina*, were primarily recorded in pine, mixed and acidophilous deciduous forests. The lowest contribution of small balsam to the neophytization of forest communities in Silesian Upland was observed in coniferous and mixed coniferous forests (Fig. 37).
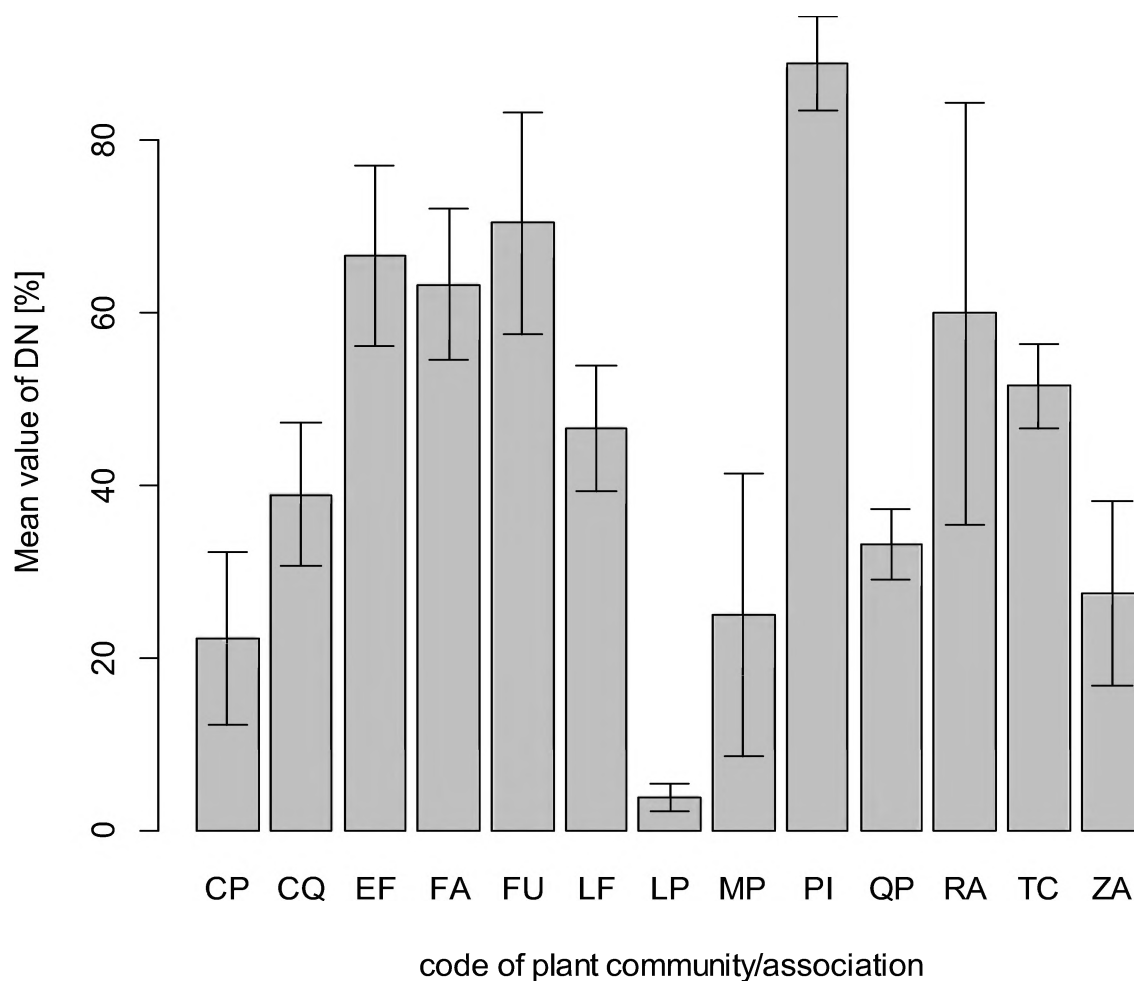
Fig. 36. Comparison of degree of neophytization D_N (ratio of cover of alien to cover of all species) among the vegetation units that had been distinguished in the Silesian Upland. Explanations: CP – *Calamagrostio villosae-Pinetum*; CQ – *Calamagrostio-Quercetum;* EF – *Fagenion;* FA – *Fraxino-Alnetum;* FU – *Ficario-Ulmetum*; LF – *Luzulo pilosae-Fagetum*; LP – *Leucobryo-Pinetum*; MP – *Molinio-Pinetum*; PI – anthropogenic community with *P. sylvestris;* QP – *Querco roboris-Pinetum*; RA – *Ribeso nigri-Alnetum*; TC – *Tilio-Carpinetum*; ZA – anthropogenic community of *Querco-Fagetea* class

The pattern for *Quercus rubra*, which sometimes forms monospecific associations, is the reverse (Chmura (2013,2014). A negative correlation was found between the cover of *Quercus rubra* and the cover of *I. parviflora* (Tokarska-Guzik *et al.* 2007). It was stressed that when compared to other regions in the country, the Silesian Upland belongs to areas that are especially vulnerable to invasions of alien plant species. Such a frequent occurrence in forests in the southern part of Poland is the consequence of forest management in the past in both the case of *Q. rubra* and *P. serotina,* (Tokarska-Guzik 2005a,b). Black cherry was recommended and cultivated as an admixture and pioneer species in tree stands (Halarewicz 2011).
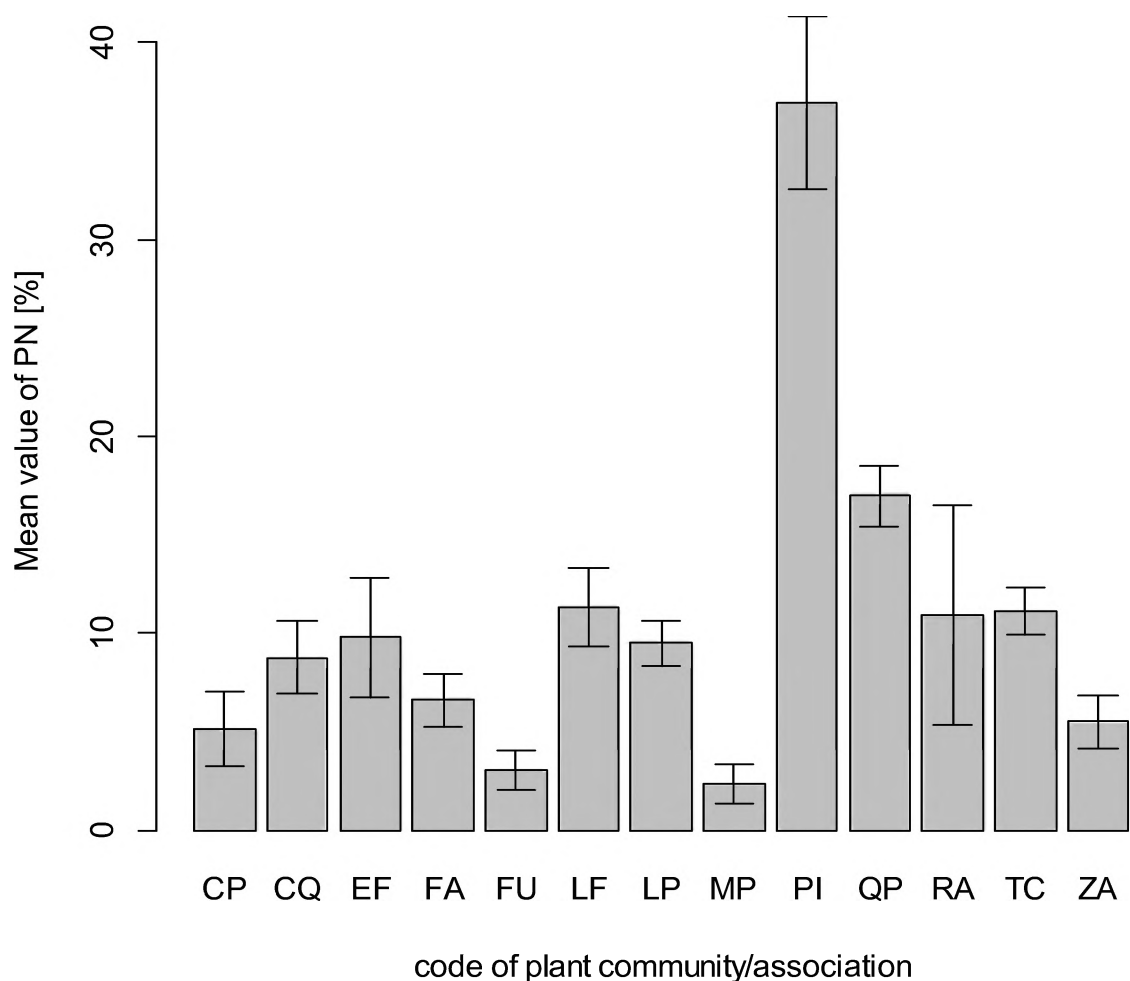
Fig. 37. Comparison of the participation in neophytization P_N (ratio of the cover of a species to the cover of all alien species) of *I. parviflora* among the vegetation units that had been distinguished in the Silesian Upland. Explanations: CP – *Calamagrostio villosae-Pinetum*; CQ – *Calamagrostio-Quercetum;* EF – *Fagenion;* FA – *Fraxino-Alnetum;* FU – *Ficario-Ulmetum*; LF – *Luzulo pilosae-Fagetum*; LP – *Leucobryo-Pinetum*; MP – *Molinio-Pinetum*; PI – anthropogenic community with *P. sylvestris;* QP – *Querco roboris-Pinetum*; RA – *Ribeso nigri-Alnetum*; TC – *Tilio-Carpinetum*; ZA – anthropogenic community of *Querco-Fagetea* class

As a result, the more frequent occurrence of *Q. rubra* in habitats of coniferous or mixed forests is a result of the choice of foresters to plant this tree in these types of soil rather than being an effect of the habitat preferences of the species (Otręba and Ferchmin 2007). The two most frequent and abundant tree species followed by small balsam were introduced intentionally. Unfortunately, because they migrated from the cultivation sites and spontaneously spread, their massive presence is chiefly the result of forest management. It is very often found that their common coexistence is not the result of an invasion meltdown or an invasion complex (Richardson *et al.* 2011 and literature cited therein) but the consequence of human activity.

3.3.2. Dynamics of abundance of populations in various plant communities

Year-to-year changes

On three of the ten study plots significant differences were found in the density of individuals of *Impatiens parviflora* between two consecutive years. On study plots 2 and 9, an increase in the mean density was observed in the following year but on study plot 6, there was a significant decrease in mean density of plants (Tab. 22).

In the common subplots, significant changes were observed on five of the study plots – on study plots 1, 2, 9 an increase of density was noted and on study plots 4, 6 the mean density decreased significantly (Tab. 22). In some cases plants grew on different subplots (i.e. study plots 3 and 8) when compared to the previous year, so there were no common subplots at all.

Tab. 22. Differences in mean density of *Impatiens parviflora* on study plots (*U* Mann-Whitney test) and common subplots between two subsequent years (Wilcoxon test)

Study Plot		Total		Common subplots	
	Year	Mean±SD	P	Mean±SD	P
1	2005	19.58±12.83	ns	19.8±12.7	0.0009712
	2006	19.36±14.27		22.1±13.4	
2	2005	5.35±3.31	0.036	4.0±3.0	<0.0001
	2006	10.15±9.87		5.8±5.4	
3	2005	1.5±0.53	ns	-	
	2006	1.83±1.60		-	
4	2005	5.24±3.62	ns	5.5±3.7	0.03585
	2006	4.52±3.52		4.5±3.5	
5	2005	6.89±6.80	ns	10.0±7.4	ns
	2006	7.2±6.16		8.2±6.5	
6	2005	29.28±11.18	<.0001	30.1±10.8	<0.0001
	2006	20.78±12.63		20.3±12.5	
7	2005	17.36±10.92	ns	18.0±10.8	ns
	2006	23.99±20.06		24.8±19.9	
8	2005	1.56±0.88	ns	-	
	2006	9.33±11.31		-	
9	2005	4.72±5.22	0.034	4.8±5.5	ns
	2006	6.2±4.98		5.4±4.7	
10	2005	4.05±3.03	ns	5.4±3.3	0.0199
	2006	5.09±4.91		13.4±10.7	

Under favorable conditions small balsam can markedly increase in cover year by year. Obidziński and Symonides (2000) noted an increase in both cover and density (number of individuals) in six types of communities – *Tilio-Carpinetum* and *Ficario-Ulmetum campestris* and their degraded variants. It is noteworthy that they chose patches of vegetation that had been established perpendicular to the forest path, thus the distinct gradient of the disturbance was apparent in this research. In the present study non-significant changes occurred on two plots of the

initial invasion group and one from the intermediate group. A significant decrease occurred on only one study plot from the intermediate invasion group. Significant changes in the mean cover were observed more frequently on the common subplots on which individuals had been present in the previous year except for one study plot. It can be inferred that patches of *I. parviflora* generally persisted where it had been before in this study, which may be the result of favorable microsites, lower biocenotic resistance or short-distance dispersal.

Long term changes

During the eight years of the study from 2005 until 2012, the spatial distribution (Fig. 38–47), frequency and mean cover (Fig. 48–51) of *Impatiens parviflora* changed considerably on permanent study plots. The frequency, i.e. the number of subplots that were occupied by small balsam within the study plots changed significantly in seven cases (Tab. 23). The Friedman rank test revealed significant changes in the mean cover in paired subplots within all of the study plots except for study plot 3. The Kruskal-Wallis test indicated the significance of the mean cover changes in all of the study plots except for study plots 3, 5, 7 and 8 (Tab. 24).

On study plot 1, which was growing near a floodplain forest *Fraxino-Alnetum* and which represented an intermediate degree of invasion, there was an increase in the frequency of *I. parviflora* at the beginning of the study but it later decreased systematically from 75% down to 10%. Meanwhile, the mean cover of the invaded subplots decreased from 40% to ca. 5% (Fig. 48AB). The distribution of individuals also changed. At the beginning of the study, the spatial structure was gradient but later on it became scattered (Fig. 38).

Study plot 2, which was situated in an oak-hornbeam forest, also underwent significant changes. Two peaks in the increase in the frequency of small balsam occurred in 2007 and 2010 when the number of invaded subplots varied between 79 and 71. The mean frequency was ca. 54% but in the last year of the study, there were only 18, which was the lowest value during the entire period of the research (Fig. 48CD). The median cover was similar during the eight years and amounted to 10%, although it decreased to ca. 5% in the invaded subplots in the last two years. Study plot 3, which was from the initial invasion group and was situated in a beech wood *Dentario glanduloase-Fagetum*, resembled *Carici-Fagetum* and was characterized by either random dynamics in the frequency of small balsam, which ranged from five to ten, while its median cover in invaded subplots decreased somewhat from 8% down to 5% (Fig. 48EF). The population was characterized by a scattered type of distribution (Fig. 40).

Study plot 4 was highly invaded at the beginning of the study and therefore it represented a saturation invasion group. This area was an oak-hornbeam forest in which there was a rapid

decrease in the frequency of *I. parviflora* from 90 down to 24 (Fig. 49A). The highest median cover was observed in the years 2007–2011 but in the last year of the study, it dropped to ca. 5% (Fig. 49B). The spatial distribution of individuals changed from areal type to areal-clumped (Fig. 41).

Study plot 5 was representative of an intermediate degree of invasion and was situated in an oak-hornbeam forest. The frequency of *I. parviflora* there was highest in the first year and in last year, reaching 46 and 47, respectively. The median cover in the invaded subplots was similar over the years and varied between 10% and 15% (Fig. 49CD). The spatial distribution of the population was gradient-clumped during the entire period of the study (Fig. 42).

On study plot 6 a considerable decrease in the frequency of small balsam was recorded from 98 to 20, and simultaneously the median cover in the invaded subplots dropped from 70% to 10% (Fig. 49EF). This area represented highly invaded areas and was located in an acidophilous beechwood *Luzulo pilosae Fagetum*. The spatial distribution changed profoundly. In the first years of the study (2005-2006), it was areal-clumped, but in the years 2007-2008 it changed into areal-tussocky. For two years (2009-2010) the spatial structure became gradient-tussocky and finally clumped-tussocky (Fig. 43).

On study plot 7, which was also a highly invaded area and represented *Dentario glanduloase-Fagetum*, no major changes in frequency were observed except for 2010 when the number of subplots that were invaded by *I. parviflora* dropped from 95 to 79 (Fig. 50A). The median cover of small balsam varied from 15% to 20% (Fig. 50B). The distribution of individuals of small balsam was similar over the years and resembled a gradient-tussocky type of structure (Fig. 44).

Study plot 8 was situated in *Dentario glandulosae-Fagetum*, which at the beginning of the study was in the initial phase of an invasion and subsequently underwent significant changes in the frequency of *I. parviflora*, which increased significantly from 9 to 23 (Fig. 50C). The median cover in invaded subplots increased from 5% to 10% (Fig. 50D). The spatial structure of the population was rather scattered in every year of the observation (Fig. 45).

In both study plots 9 and 10, which are situated in a beechwood *Dentario glandulosae-Fagetum* and an oak-hornbeam forest *Tilio-Carpinetum*, there was an increase in the number of subplots that were invaded by small balsam. In the former from 37 to 56 were detected and in the latter, which occurred more rapidly, from 49 to 93 were detected (Fig. 50E, Fig. 51A). The spatial structure of the population on study plot 9 was of an areal type but in the last year of the study it resembled a gradient type (Fig. 46).

Tab. 23. Results of the G-test of the comparison of frequencies (number of invaded vs uninvaded subplots by *Impatiens parviflora*) in the years 2005-2012

Number of study plot	Statistics	Probability
1	169.7	<0.000
2	124.4	<0.000
3	4.0	ns
4	175.7	<0.000
5	12.3	ns
6	333.7	<0.000
7	28.6	0.00017
8	28.0	0.00021
9	11.0	ns
10	61.4	<0.000

Tab. 24. Results of Friedman rank test (all subplots included) and Kruskal-Wallis test (only invaded plots) on the basis of comparison of *Impatiens parviflora* mean cover over the years 2005-2012

No. of study plot	Friedman rank test	Kruskal-Wallis test
1	$\chi2$=306.9; p <0.0001	$\chi2$= 82.3; p < 0.0001
2	$\chi2$=223.6; p <0.0001	$\chi2$= 16.0; p = 0.02441
3	$\chi2$= 6.0663; ns	$\chi2$= 7.59; ns
4	$\chi2$= 172.5; p <0.0001	$\chi2$= 81.5; p<0.0001
5	$\chi2$= 105.4; p <0.0001	$\chi2$=6.0; ns
6	$\chi2$= 418.0; p <0.0001	$\chi2$=158.6; p< 0.0001
7	$\chi2$= 32.21; p <0.0001	$\chi2$= 1.8; ns
8	$\chi2$=37.2; p <0.0001	$\chi2$=6.0; ns
9	$\chi2$=306.9; p <0.0001	$\chi2$=27.0; p = 0.00032
10	$\chi2$=105.4; p <0.0001	$\chi2$= 22.1; p = 0.0023

Fig. 38. Dynamics of distribution of *Impatiens parviflora* on study plot no. 1. Explanations: 1–0%; 2– >1-10%; 3– >10-20%; 4– >20-30%; 5– >30-40%; 6– >40-50%; 7– >50-60%; 8– >60-70%; 9– >70%; 10– >80% of plant cover

Fig. 39. Dynamics of distribution of *Impatiens parviflora* on study plot no. 2. Explanations: 1–0%; 2– >1-10%; 3– >10-20%; 4– >20-30%; 5– >30-40%; 6– >40-50%; 7– >50-60%; 8– >60-70%; 9– >70%; 10– >80% of plant cover

Fig. 40. Dynamics of distribution of *Impatiens parviflora* on study plot no. 3. Explanations: 1–0%; 2– >1-10%; 3– >10-20%; 4– >20-30%; 5– >30-40%; 6– >40-50%; 7– >50-60%; 8– >60-70%; 9– >70%; 10– >80% of plant cover
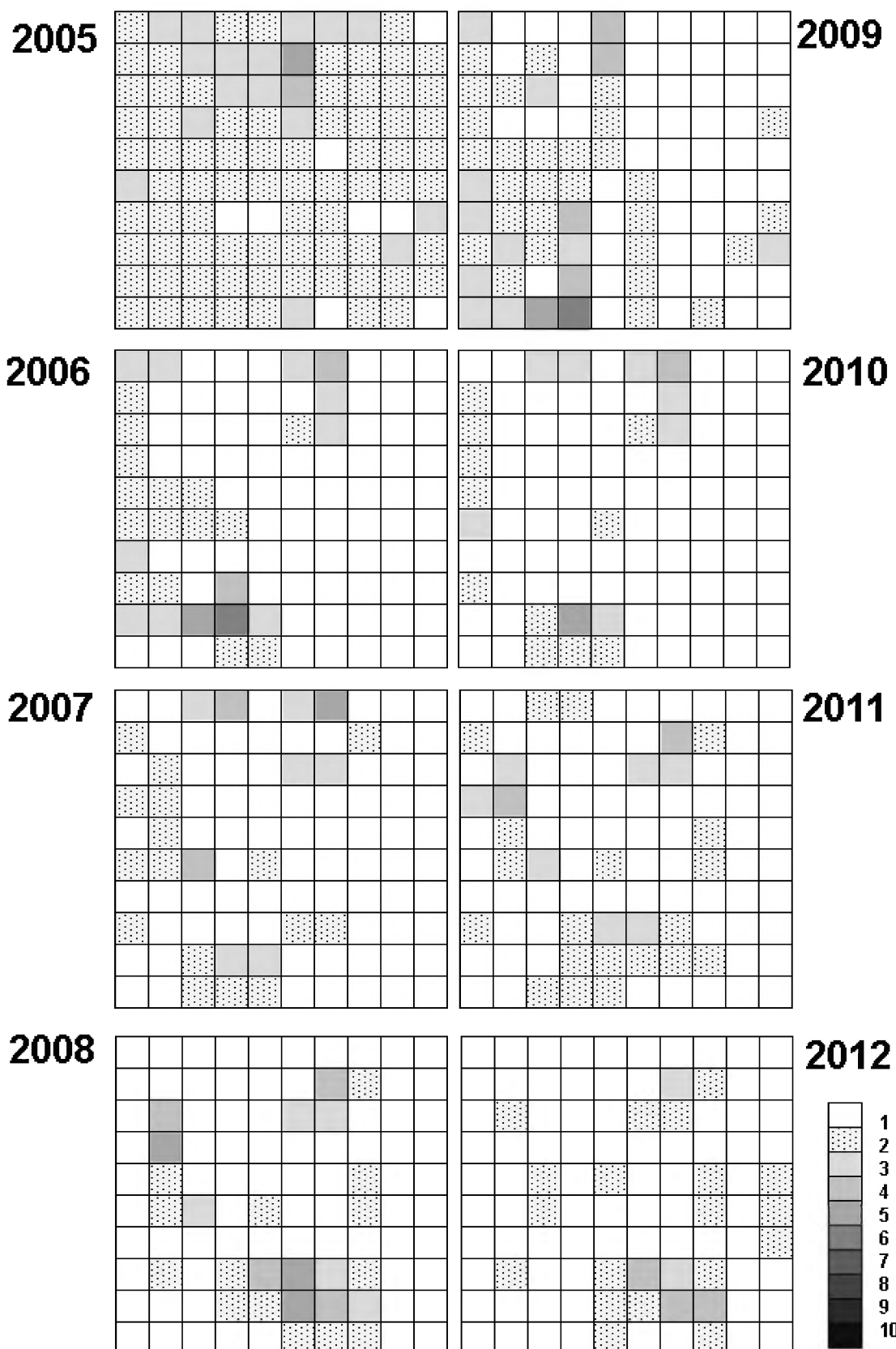
Fig. 41. Dynamics of distribution of *Impatiens parviflora* on study plot no. 4. Explanations: 1–0%; 2– >1-10%; 3– >10-20%; 4– >20-30%; 5– >30-40%; 6– >40-50%; 7– >50-60%; 8– >60-70%; 9– >70%; 10– >80% of plant cover
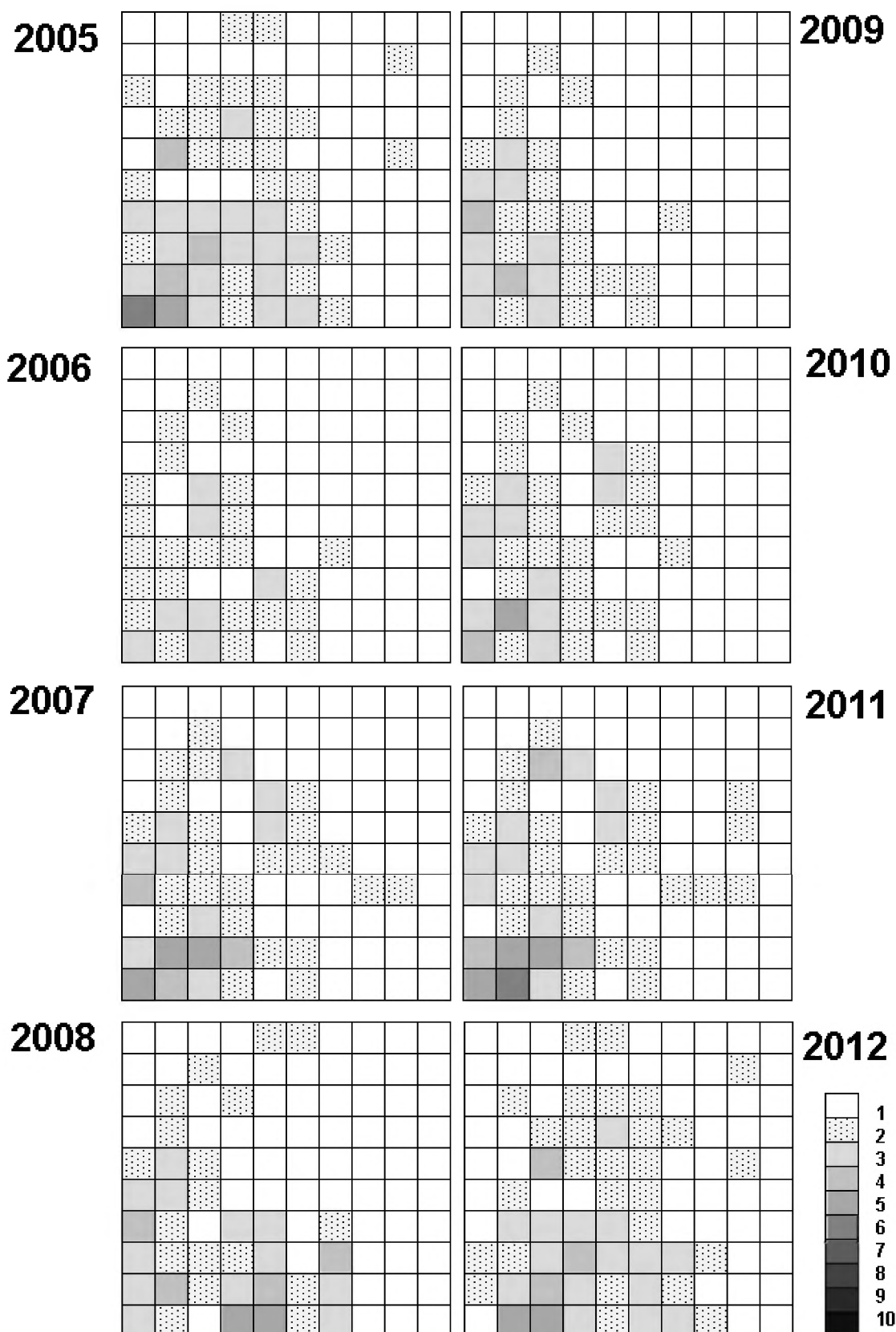
Fig. 42. Dynamics of distribution of *Impatiens parviflora* on study plot no. 5. Explanations: 1–0%; 2– >1-10%; 3– >10-20%; 4– >20-30%; 5– >30-40%; 6– >40-50%; 7– >50-60%; 8– >60-70%; 9– >70%; 10– >80% of plant cover
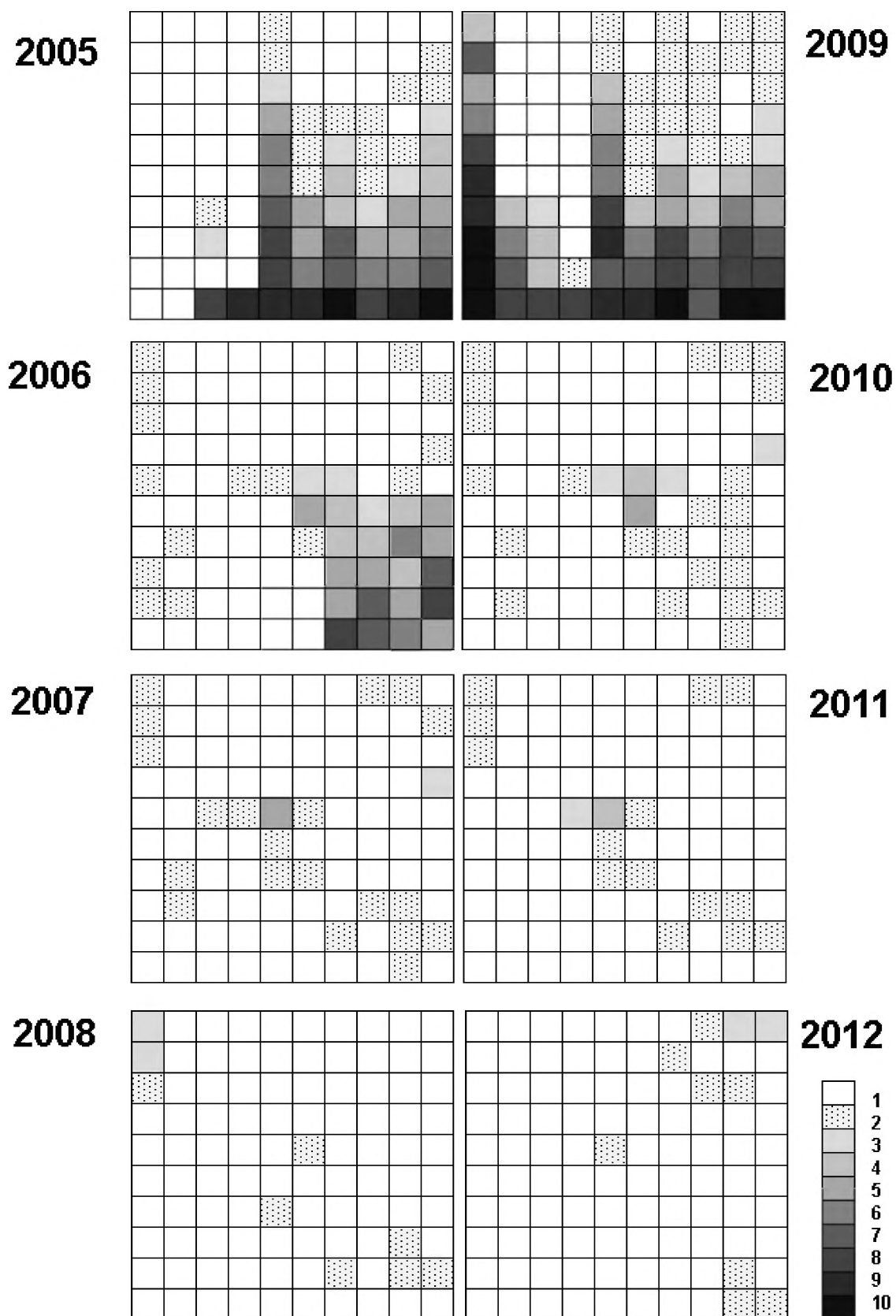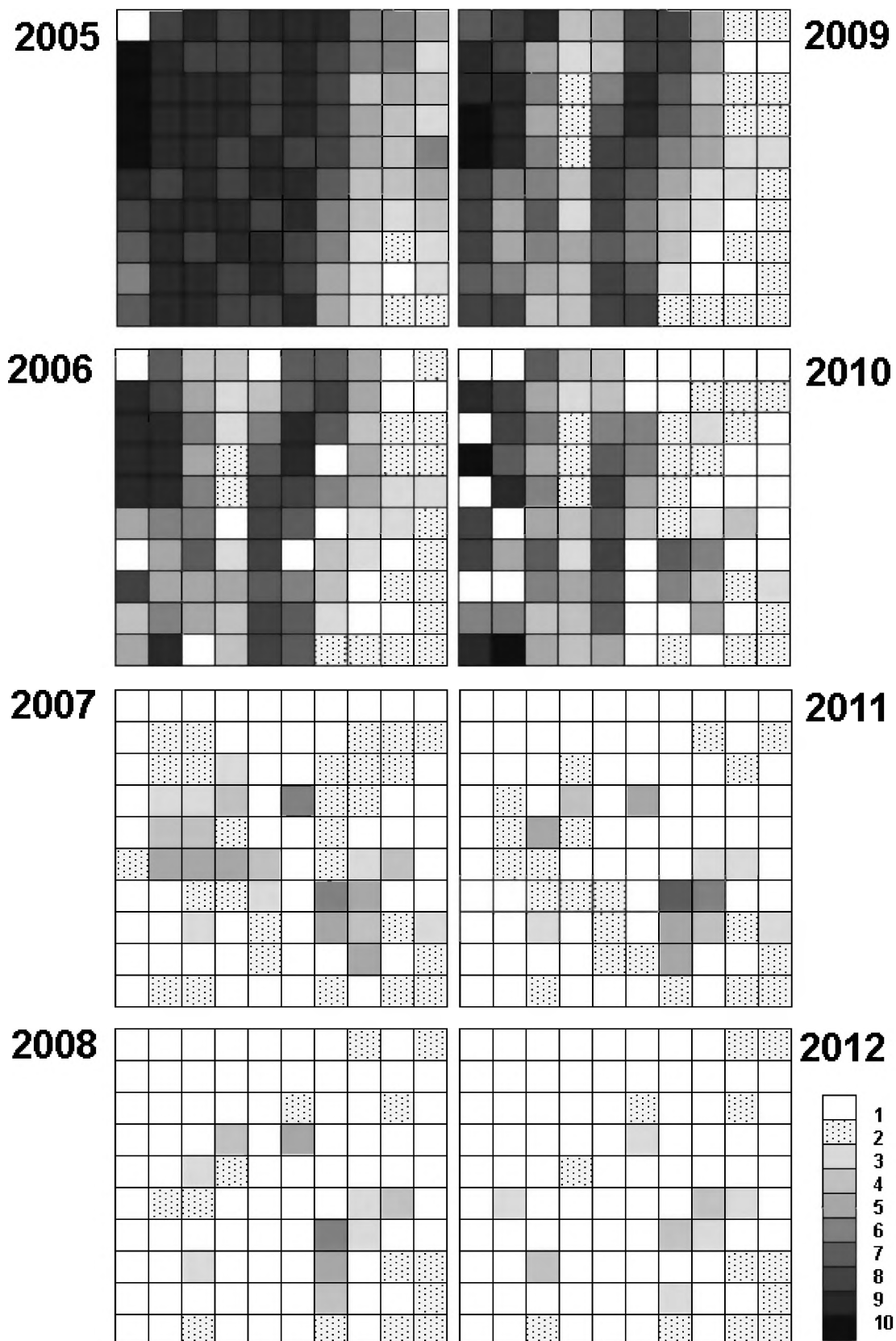
Fig. 43. Dynamics of distribution of *Impatiens parviflora* on study plot no. 6. Explanations: 1–0%; 2– >1-10%; 3– >10-20%; 4– >20-30%; 5– >30-40%; 6– >40-50%; 7– >50-60%; 8– >60-70%; 9– >70%; 10– >80% of plant cover
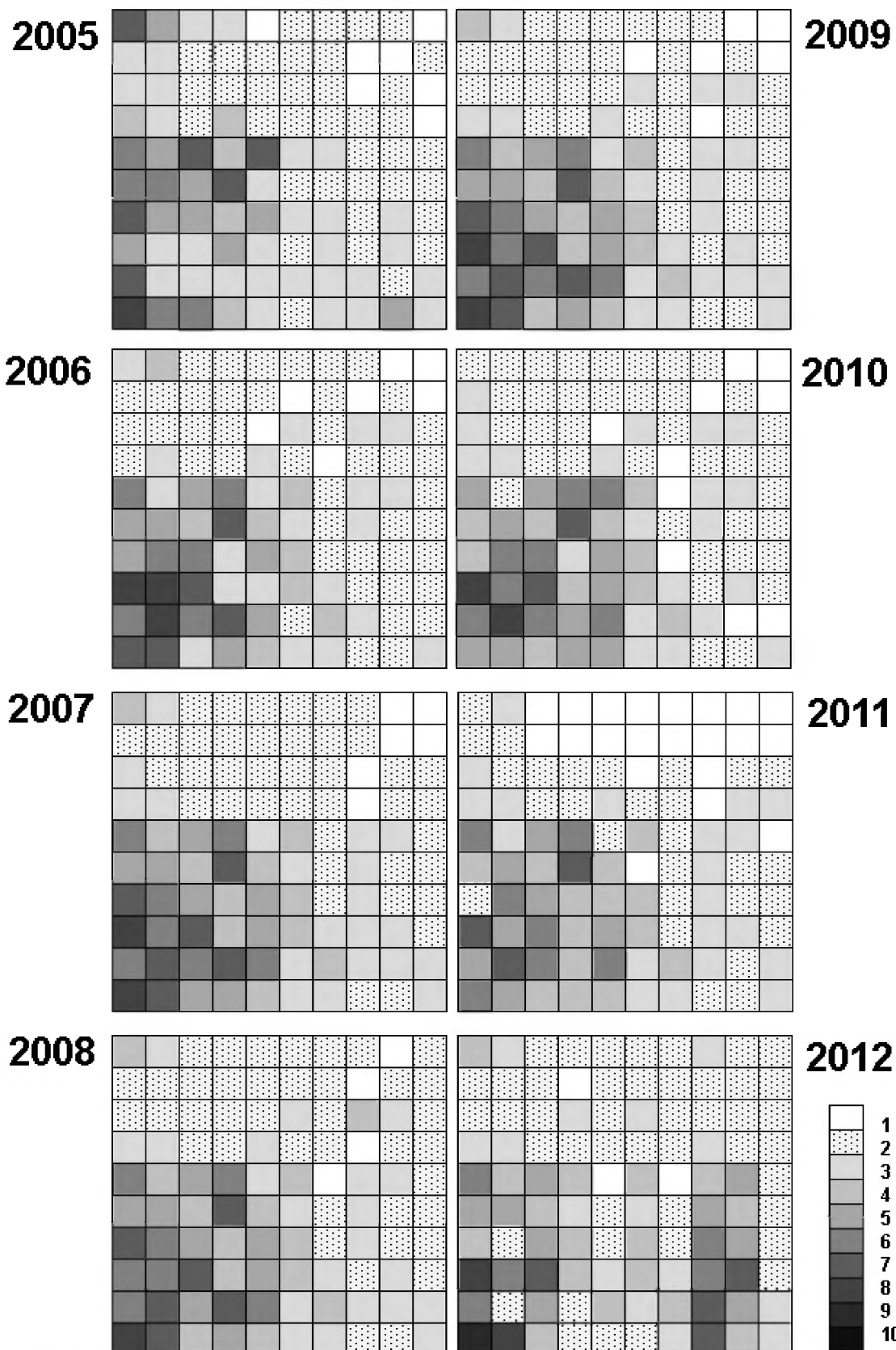
Fig. 44. Dynamics of distribution of *Impatiens parviflora* on study plot no. 7. Explanations: 1– 0%; 2– >1-10%; 3– >10-20%; 4– >20-30%; 5– >30-40%; 6– >40-50%; 7– >50-60%; 8– >60-70%; 9– >70%; 10– >80% of plant cover
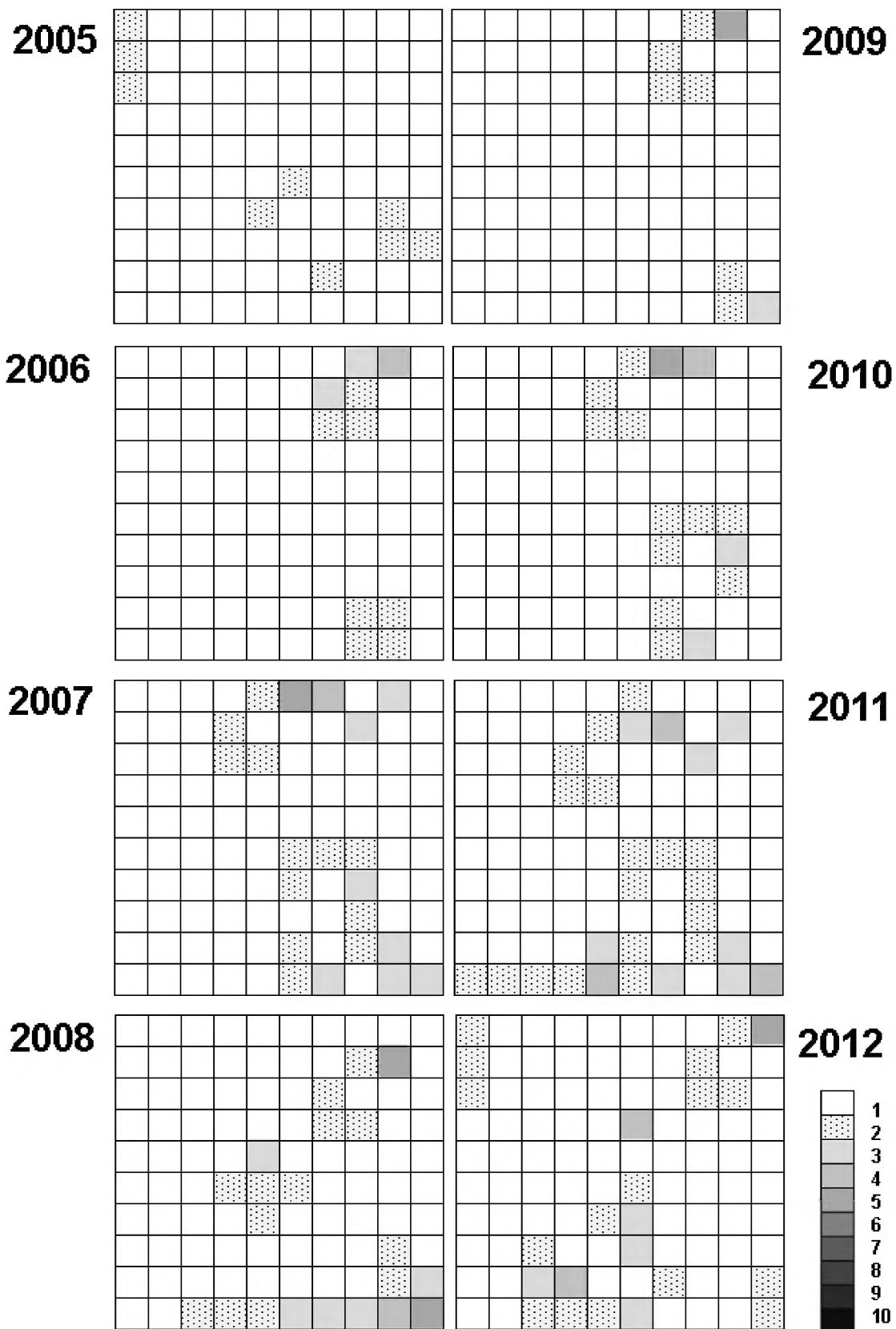
Fig. 45. Dynamics of distribution of *Impatiens parviflora* on study plot no. 8. Explanations: 1–0%; 2– >1-10%; 3– >10-20%; 4– >20-30%; 5– >30-40%; 6– >40-50%; 7– >50-60%; 8– >60-70%; 9– >70%; 10– >80% of plant cover
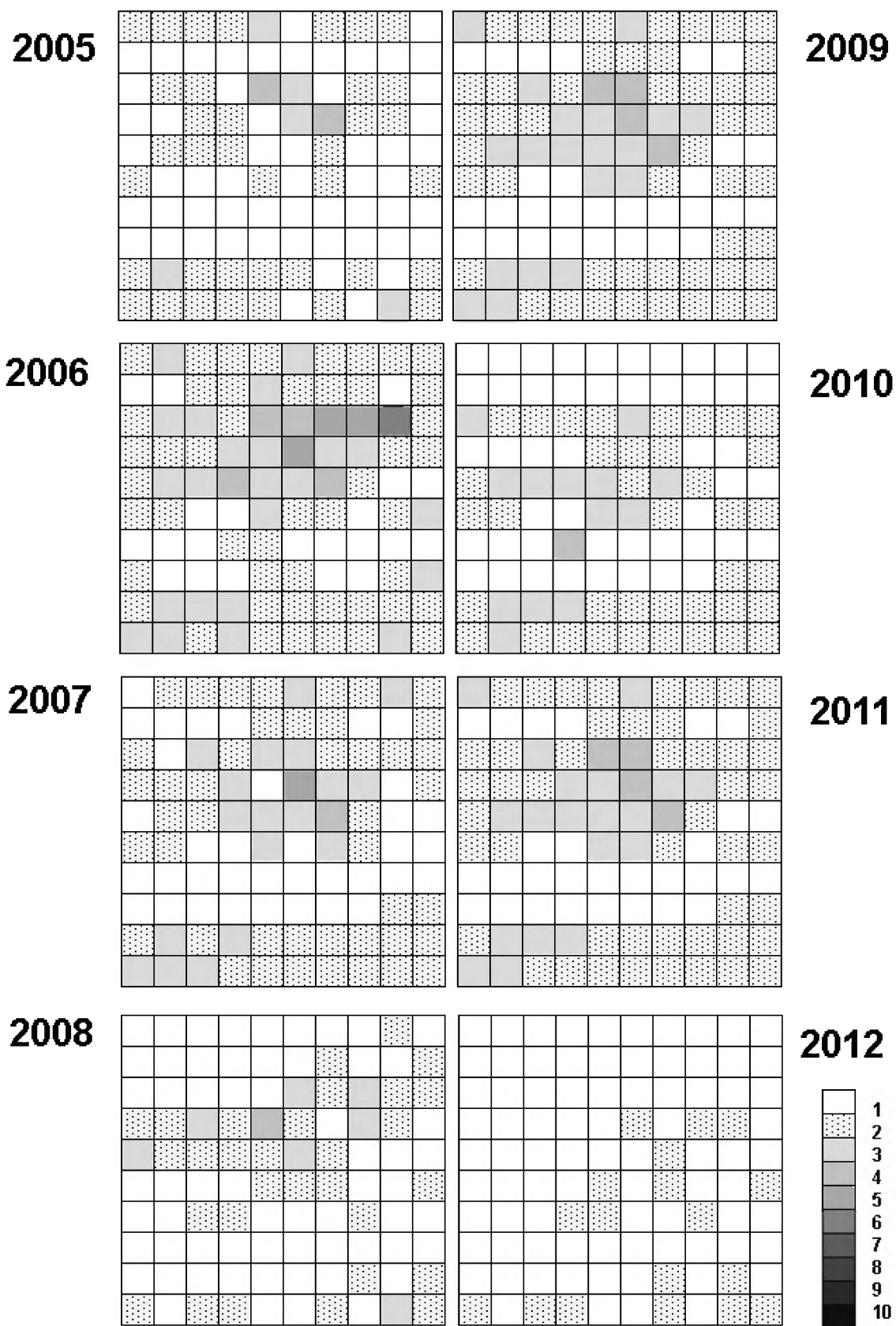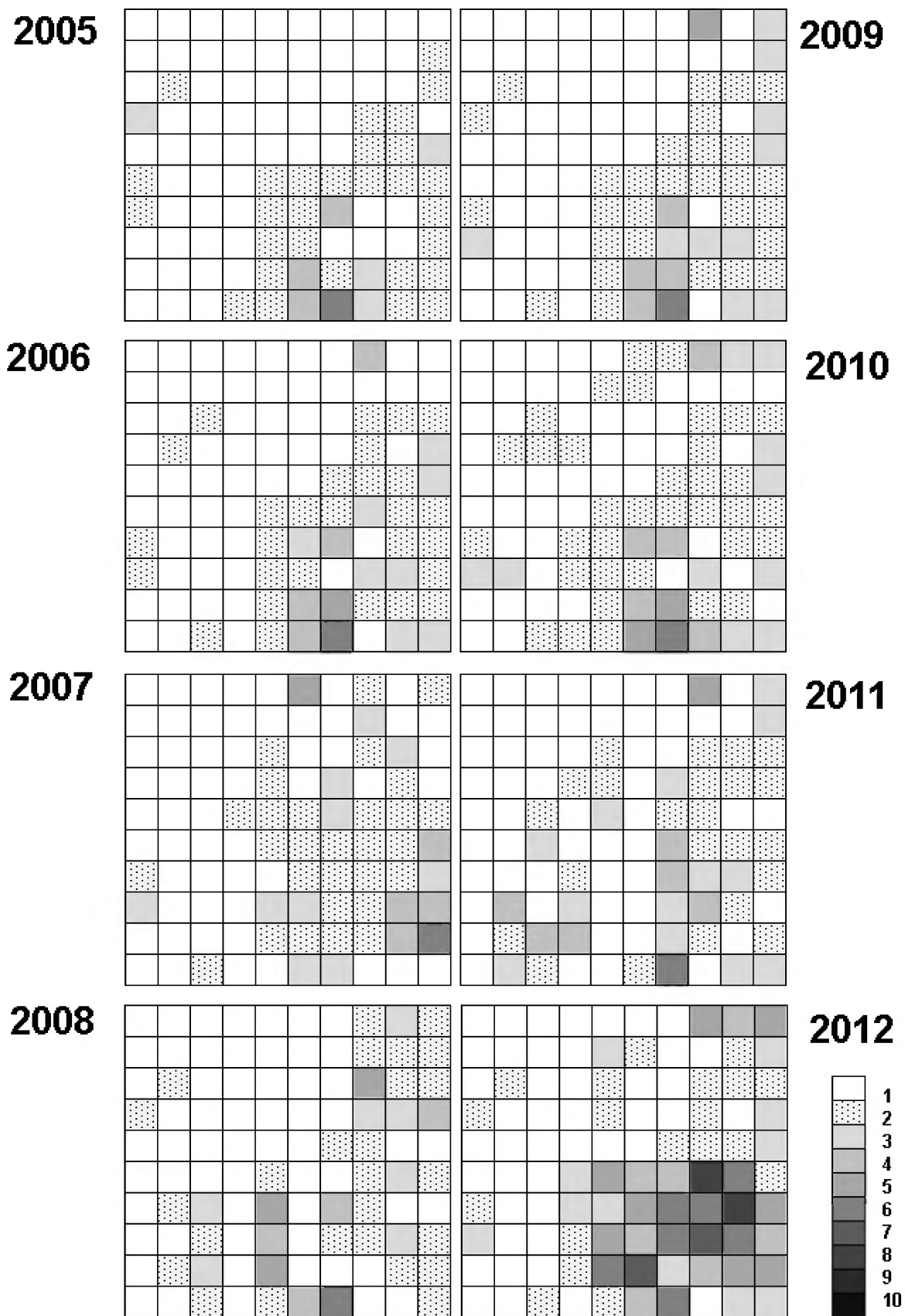
Fig. 46. Dynamics of distribution of *Impatiens parviflora* on study plot no. 9. Explanations: 1–
0%; 2– >1-10%; 3– >10-20%; 4– >20-30%; 5– >30-40%; 6– >40-50%; 7– >50-60%; 8– >60-70%;
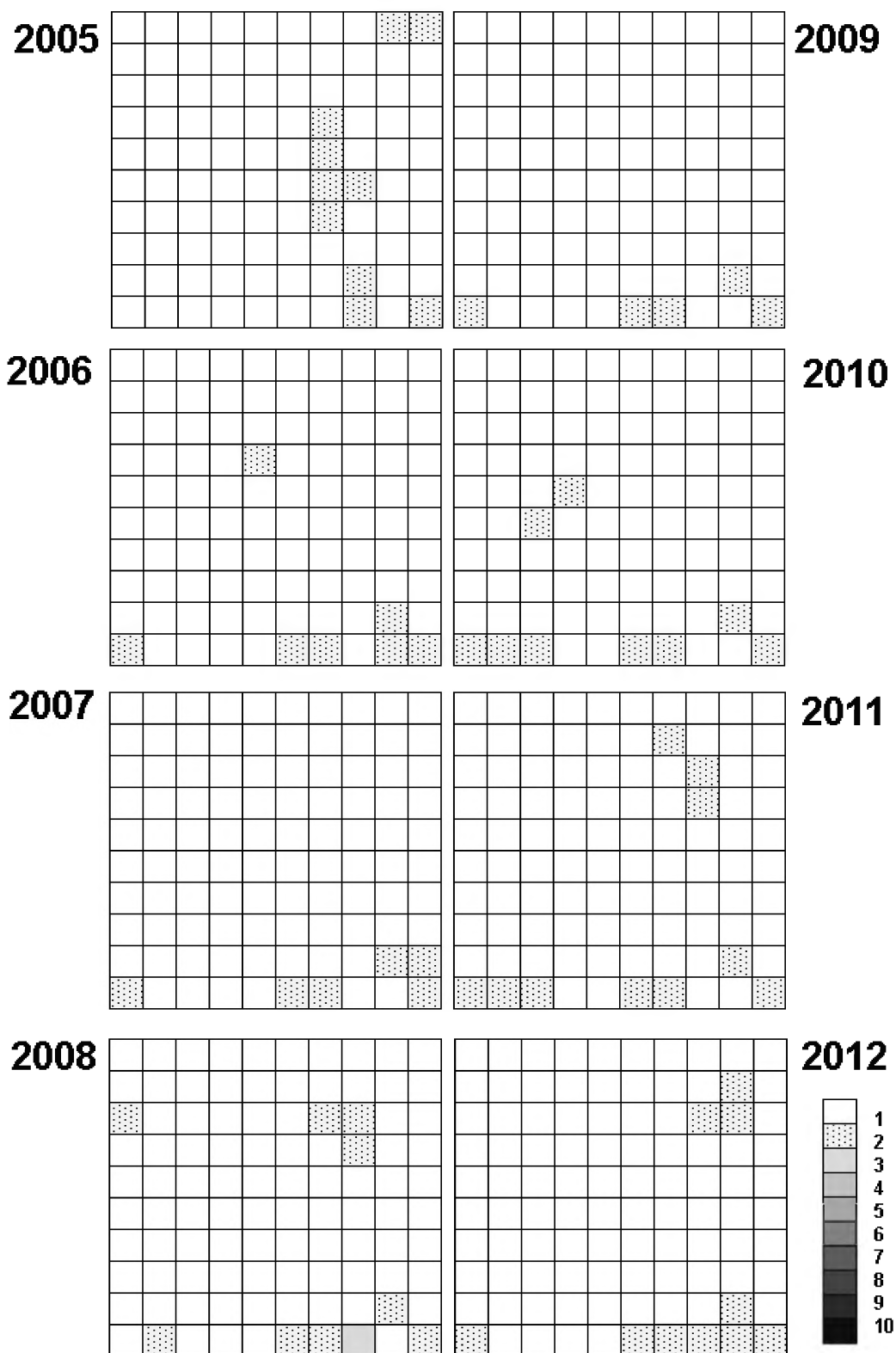9– >70%; 10– >80% of plant cover

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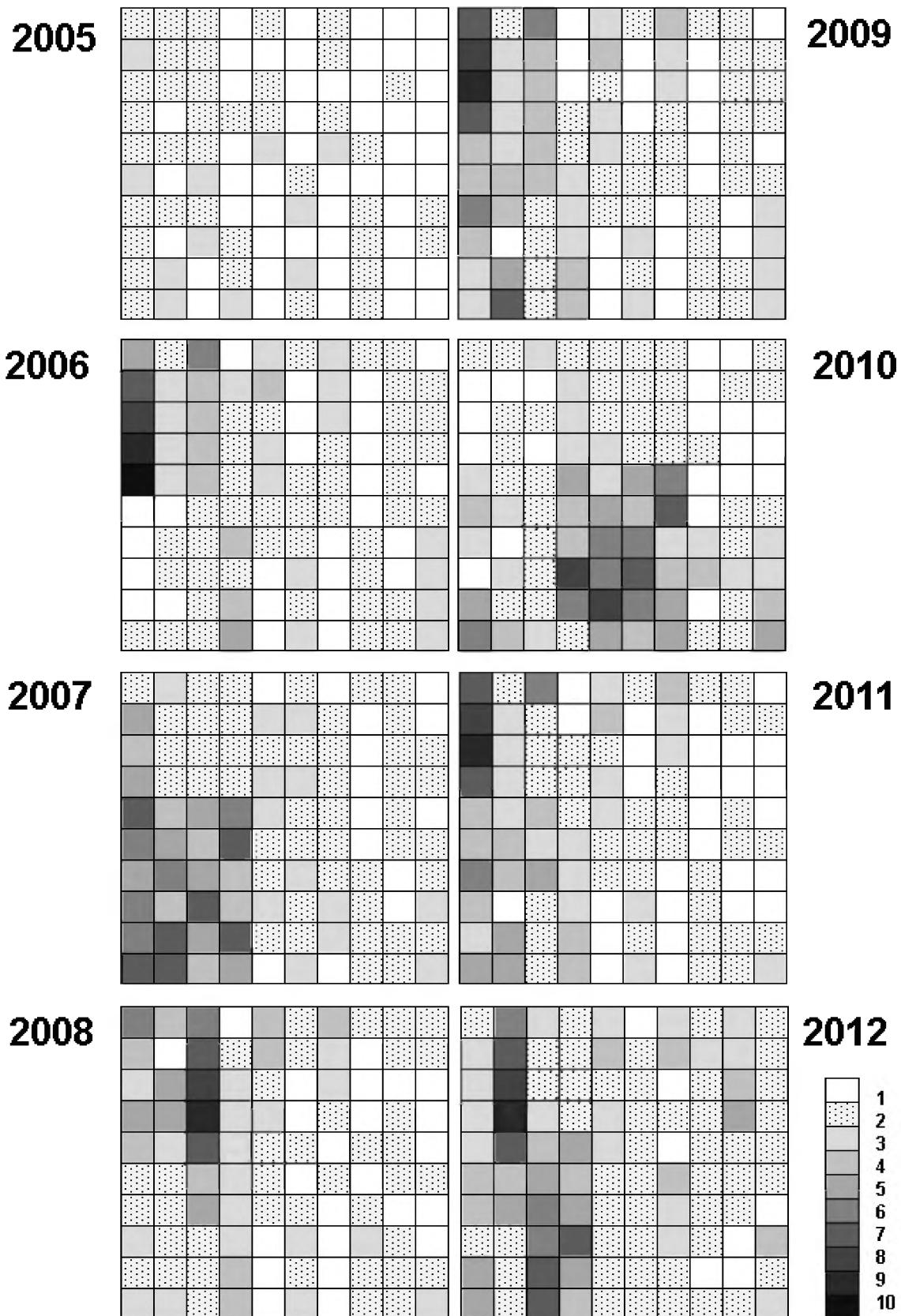
Fig. 47. Dynamics of distribution of *Impatiens parviflora* on study plot no. 10. Explanations: 1–0%; 2– >1-10%; 3– >10-20%; 4– >20-30%; 5– >30-40%; 6– >40-50%; 7– >50-60%; 8– >60-70%; 9– >70%; 10– >80% of plant cover
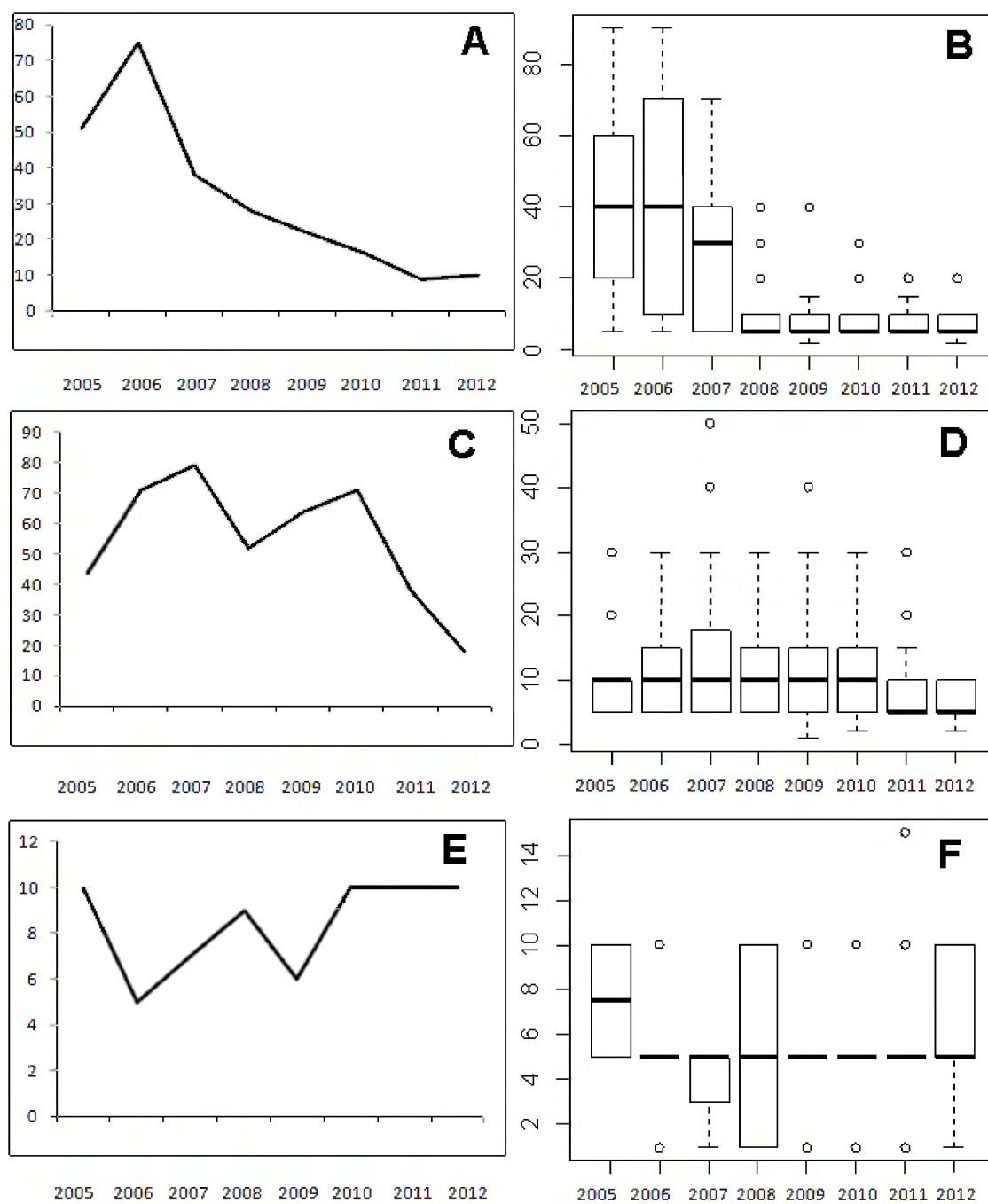
Fig. 48. Dynamics of the frequency (left) and the median percent cover (right) only in subplots that were occupied by *Impatiens parviflora*. Explanations AB – study plot 1, CD – study plot 2, EF – study plot 3
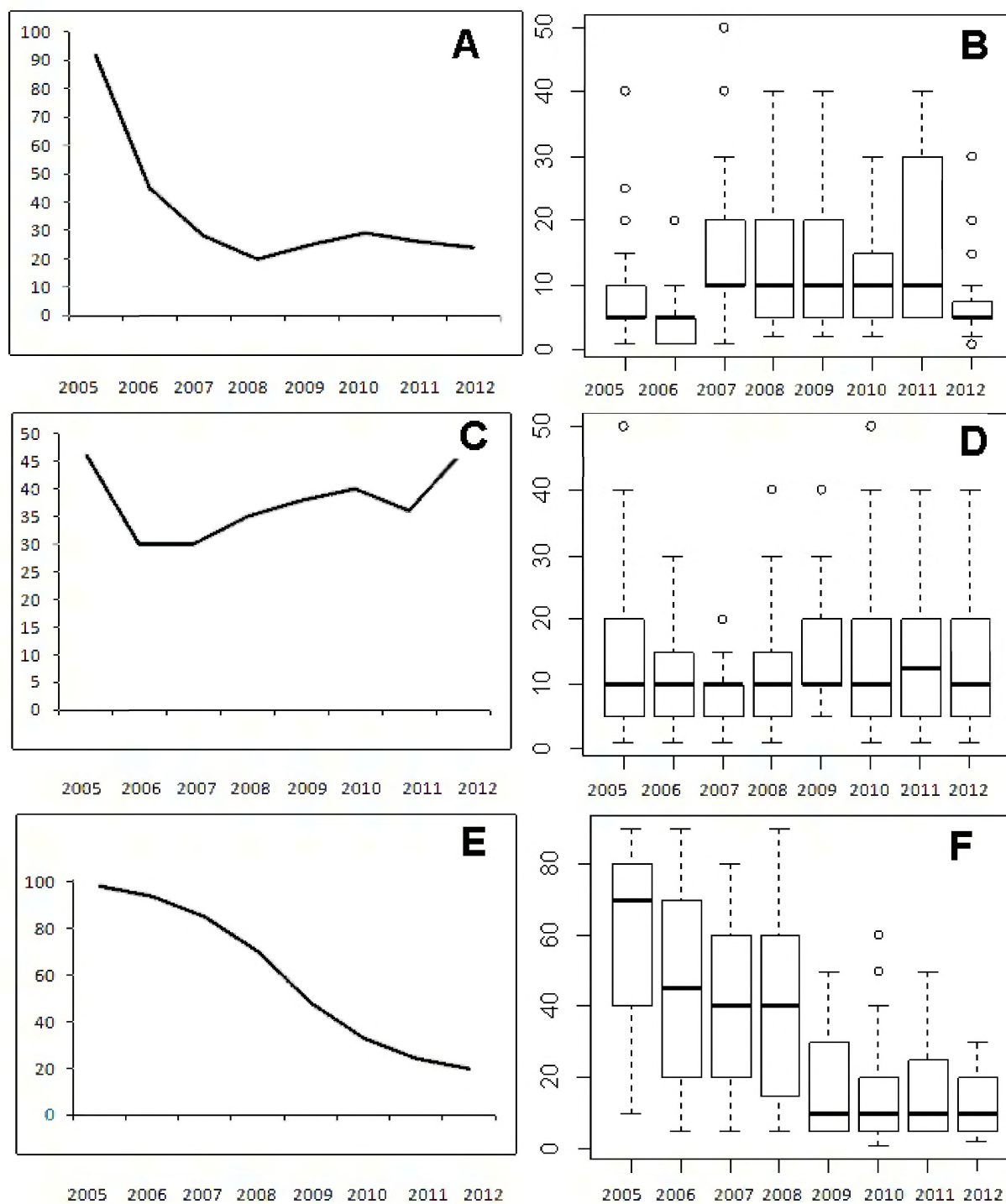
Fig. 49. Dynamics of the frequency (left) and the median percent cover (right) only in subplots that were occupied by *Impatiens parviflora*. Explanations AB – study plot 4, CD – study plot 5, EF – study plot 6
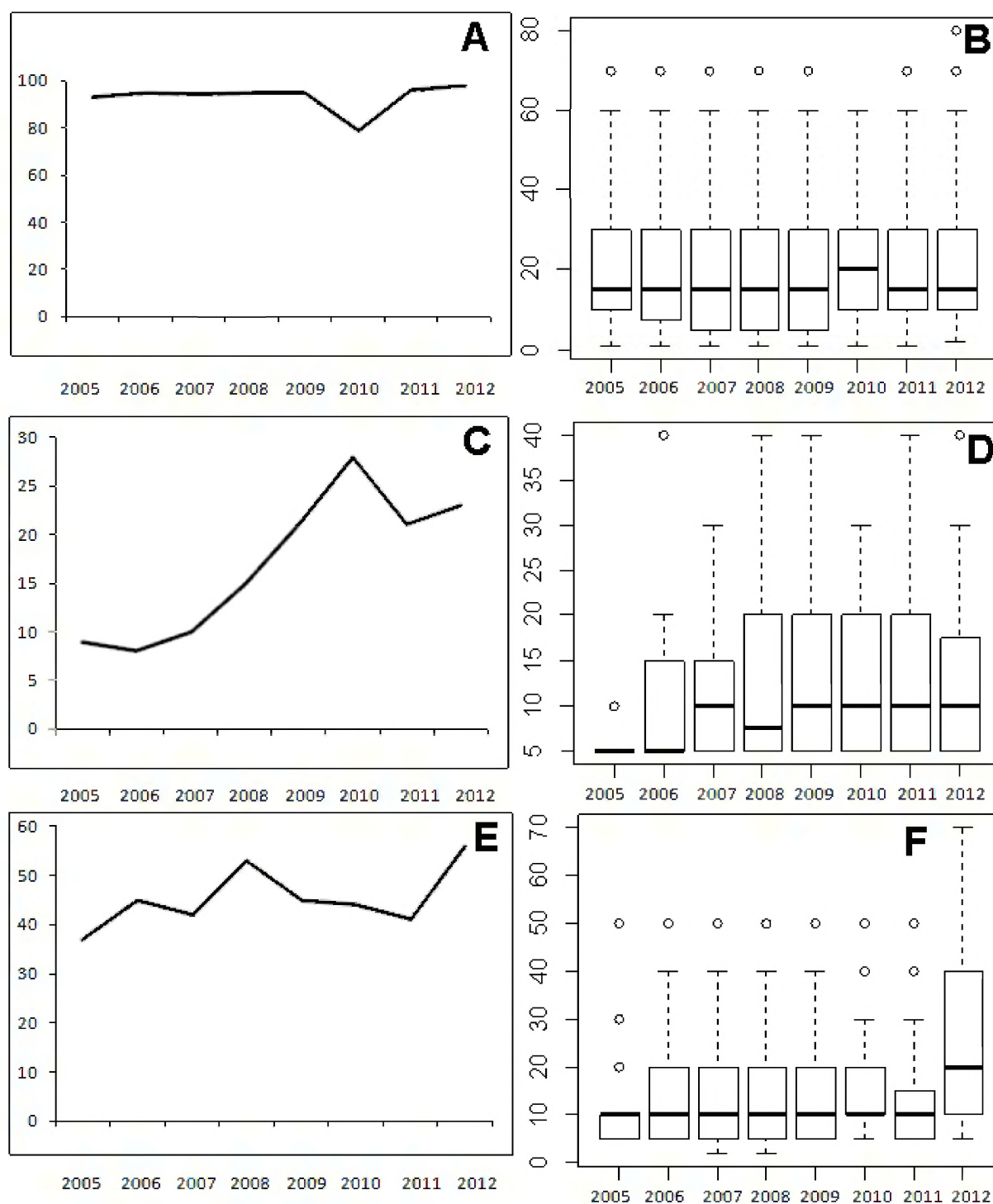
Fig. 50. Dynamics of the frequency (left) and the median percent cover (right) only in subplots that were occupied by *Impatiens parviflora*. Explanations AB – study plot 7, CD – study plot 8, EF – study plot 9

On study plot 9 the median cover increased from 10 to 20 (Fig. 50F), whereas on study plot 10, it varied over the years and ranged from 8 to 18% (Fig. 51B).
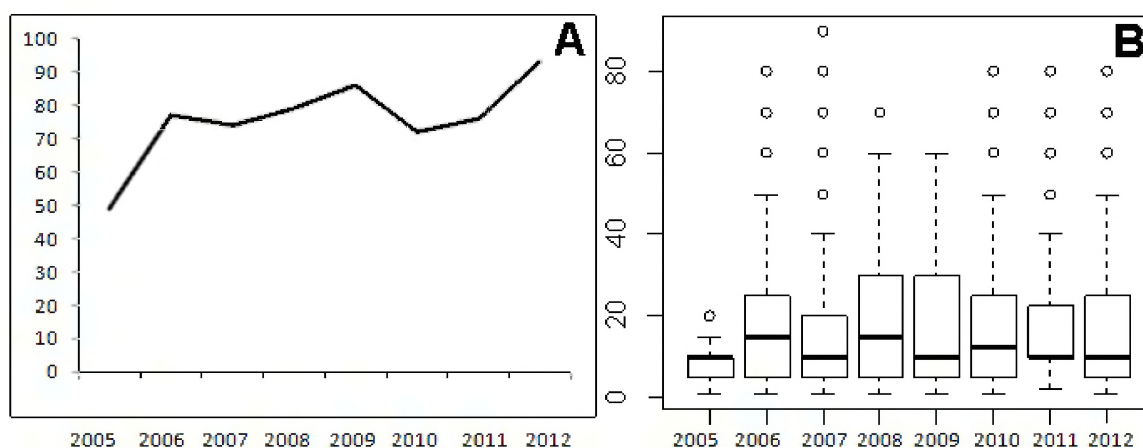
Fig. 51. Dynamics of the frequency (left) and the median percent cover (right) only in subplots that were occupied by *Impatiens parviflora*. Explanations AB – study plot 10

The spatial distribution of the population of *I. parviflora* on study plot 10 was rather scattered in 2005 but later on it started to be a gradient type (Fig. 47).

To the best of the author's knowledge, no similar studies that were designed to identify the dynamics of *I. parviflora* every year over a long period of time have been undertaken. Thus, it is impossible to compare these results with other studies. Examples of research that showed changes after some period can be found in the literature. For instance, Łysik (2008), who studied *Dentario glandulosae-Fagetum* on 23 permanent study plots in Ojców National Park, revealed that in 2003 in comparison with 1993 small balsam appeared on eight plots and occupied ca. 12% of the entire vegetation cover. Kiedrzyński *et al.* (2011) reported the appearance and increase in the cover of small balsam after 40 years in a nature reserve in Central Poland. Both cases presented "before and after studies" without investigating the dynamics of the species over the course of time. On the other hand, some reports have indicated a decrease in the cover of the species year by year. For instance, small balsam showed a downward trend and finally disappeared within five years during the recovery of beech forest (Godefroid *et al.* 2003).

All of the possible scenarios of population dynamics occurred in the present study – a significant increase, a significant decrease and no considerable changes. Two LTR plots that represented the saturation of an invasion underwent the process of a decrease in population and only one study plot from an intermediate degree of invasion showed a decrease in the frequency and median cover of small balsam. A distinct increase in the frequency and finally an increase in the median cover of the species were noted on three LTR plots – one study plot during the initial phase of an *I. parviflora* invasion that showed a distinct increase and two that were invaded to an intermediate degree showed a further increase in the invasion of the species. One of the three saturation invaded plots turned out to be relatively stable. The frequency and median cover of small balsam persisted

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at a similar level. On the other hand, one of the two initial invasion plots also underwent some fluctuations in the abundance of small balsam, and finally did not show any trend in the dynamics of population. Such patterns of the dynamics of populations may result from many intrinsic and extrinsic factors. It is not possible that there is only one scenario, i.e. a gradual invasion from introduction until post-invasion, e.g. dominance of the invader. As Hejda (2012) wrote *I. parviflora* can form dense stands locally on small spatial scales, while Vervoort and Jacquemart (2012) believe that *I. parviflora* can be limited locally by an unfavorable environment. As evidence they pointed out some plots that were still uncolonized by the species. It can be added that, apart from phenology and changes in abundance during the vegetation season, year-to-year and long-term changes can also be very marked. Usually an abundant occurrence of the species in forest interiors is temporary. The massive occurrences that are very often observed are usually in open habitats within forest complexes.

3.3.3. Role of plant functional groups and biotic diversity of plants in *Impatiens parviflora* invasion

The influence of species richness and species diversity on invasion success

When considering number of accompanying species in invaded and uninvaded subplots for both regions on sites without small balsam, there are differences. Uninvaded subplots in Silesian Upland were characterized by a higher species richness of native plants but the opposite situation was observed in Jurassic Upland (Tab. 25).

The analysis of relationship between the density of *I. parviflora* individuals and the cover of bare ground and the relation between the density of the species and the cover that was occupied by litter gave different results (Tab. 25). A cover of litter positively correlated with both the density and the cover of small balsam, whereas a cover of bare ground was negatively correlated with the cover of *I. parviflora*.

The associations between the cover of native species and the cover of *Impatiens parviflora* are different because of the regions. There was a negative relationship in the case of the nature reserves of the Jurassic Upland and a weak positive in the case of the Silesian Upland (Fig. 52) based on the data from the study plots and additional data sets. The relationship between the cover of native species and the cover of small balsam from only 68 study plots exhibited a negative correlation for the Jurassic Upland (rs=-0.19, p<0.0001) and a weak negative for the Silesian Upland (rs=-0.03, p<0.0001).

Tab. 25. Comparison of subplots with the absence and presence of *Impatiens parviflora* in the number of accompanying native species in the herb layer of two regions and the values of the Spearman rank correlation between the cover of bare ground, the cover of litter and the density and cover of *Impatiens parviflora* DC. (*p<0.05, **p<0.01, ***p<0.001)

	Absence	Presence
Jurassic Upland	5.57±2.6***	4.79±2.53
Silesian Upland	1.26±1.25	2.15±1.33***
Variable (Jurassic Upland)	Density	Percent cover
Cover of litter	0.35***	0.20**
Bare ground	ns	-0.11*
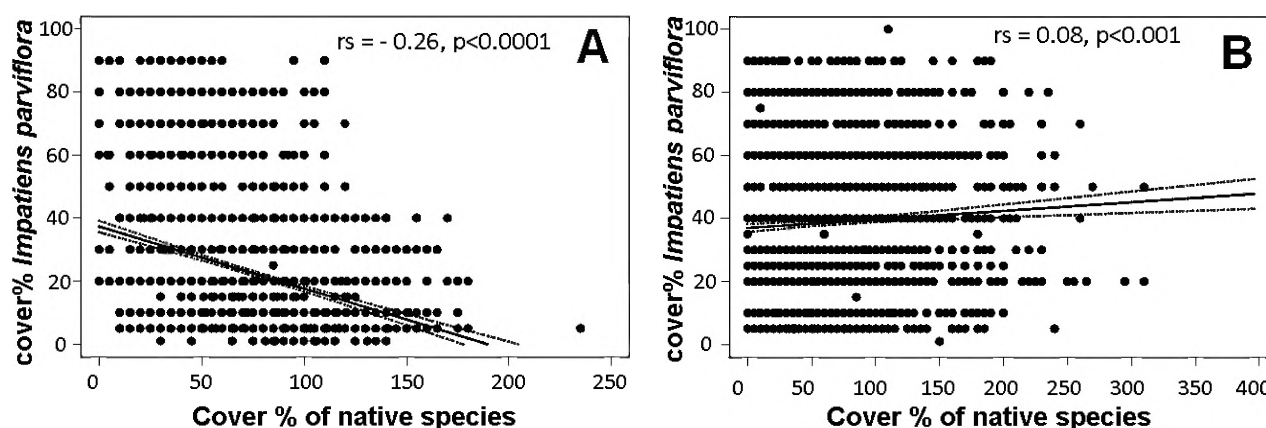
Fig. 52. Comparison of the values of Spearman rank correlation coefficient between the cover of *Impatiens parviflora* and the cover of native species for the Jurassic Upland (A) and the Silesian Upland (B) based on the data from 68 permanent study plots and additional data sets.

These aforementioned results are in accordance with findings about the relationship between the occurrence of *I. parviflora* and the presence of gaps in the ground flora layer (Obidziński, Symonides 2000), but differ in relation to the role of bare ground. It has not been confirmed that an increase in the cover of bare ground enhances an increase in the cover of the species, which Obidziński and Symoindes (2000) explained as a favorable factor for an increase in its density. However, an increase both of the cover and density on soil that is covered by litter confirmed the observation that even a thick layer of litter does not hinder the germination and growth of *I. parviflora* on the forest floor (Coombe 1956). The same result was obtained by Obidziński and Symoindes (2000), although as was already mentioned before they used transects in disturbed sites from forest paths towards forest interiors, on which the influence of the disturbance that is associated with trampling is permanent and relatively constant. In the present

work the selected study plots differed only by their level of invasion and were laid out far from forest margins such as paths, cut-areas, etc. Therefore, this indicates a more spontaneous, stochastic process that was induced by species invasiveness rather than one that was caused by extrinsic factors.

Another important feature is the biocenotic resistance of ecosystems. This character of an ecosystem or phytocoenosis is dependent on species richness and species diversity (Kennedy *et al.* 2002, Van Holle *et al.* 2003). In a previous work (Chmura, Sierka 2006a), it was shown that subplots that had been invaded by *I. parviflora* had higher biodiversity indices in relation to native species than uninvaded ones. Thus, the detailed analyses in which the two regions were analyzed separately gave different results (Fig. 52). For the Jurassic Upland there is an opposite pattern, the invaded plots had lower species richness than uninvaded. For Silesian Upland there is the other way round. This discrepancy could be explained by several factors. Firstly, forest in Jurassic Upland grow on limestone substratum, secondly the quality of forests, even in nature reserves, is better. They are less disturbed due to forest management. Thirdly, according to cadastral maps, Jurassic forests are rather ancient forest than recent forests.

Interesting results about differences in species richness and cover of species were shown by Vervoort *et al.* (2012). Both number of species and cover was lower on plots that had not been colonized by *I. parviflora* and *I. noli-tangere* when compared to sites with *I. parviflora*, whereas sites invaded only by *I. parviflora* had significantly a lower species richness than sites with *I. noli-tangere* only and plots on which two species were present. In the same study, a negative relationship between the coverage of small balsam and species richness was also shown and it was quite high (R^2 = -0.41), which indicates that *I. parviflora* preferred sites with lower species richness when compared to its native congener. Plots with two *Impatiens* species did not differ significantly in species richness and cover from plots with native balsam only.

A negative correlation between herbaceous species as well as with mosses was demonstrated by Dobravolskaitė (2012) for pine and spruce forests and pine forest edges.
Negative relations between density, the cover of small balsam and the cover of native species were revealed by Obidziński, Symonides (2000) and Csontos (1984). Godefroid and Koedam (2010) demonstrated that species richness in the herb layer significantly decreased with an increasing abundance of *I. parviflora*. The opposite pattern was found in an analysis of cover relations. *I. parviflora* had its highest abundance in communities that had a dense herb layer. Golivets (2013) found a very weak positive (r=0.12) but significant correlation between the abundance of small balsam and other species at the scale of $1m^2$.
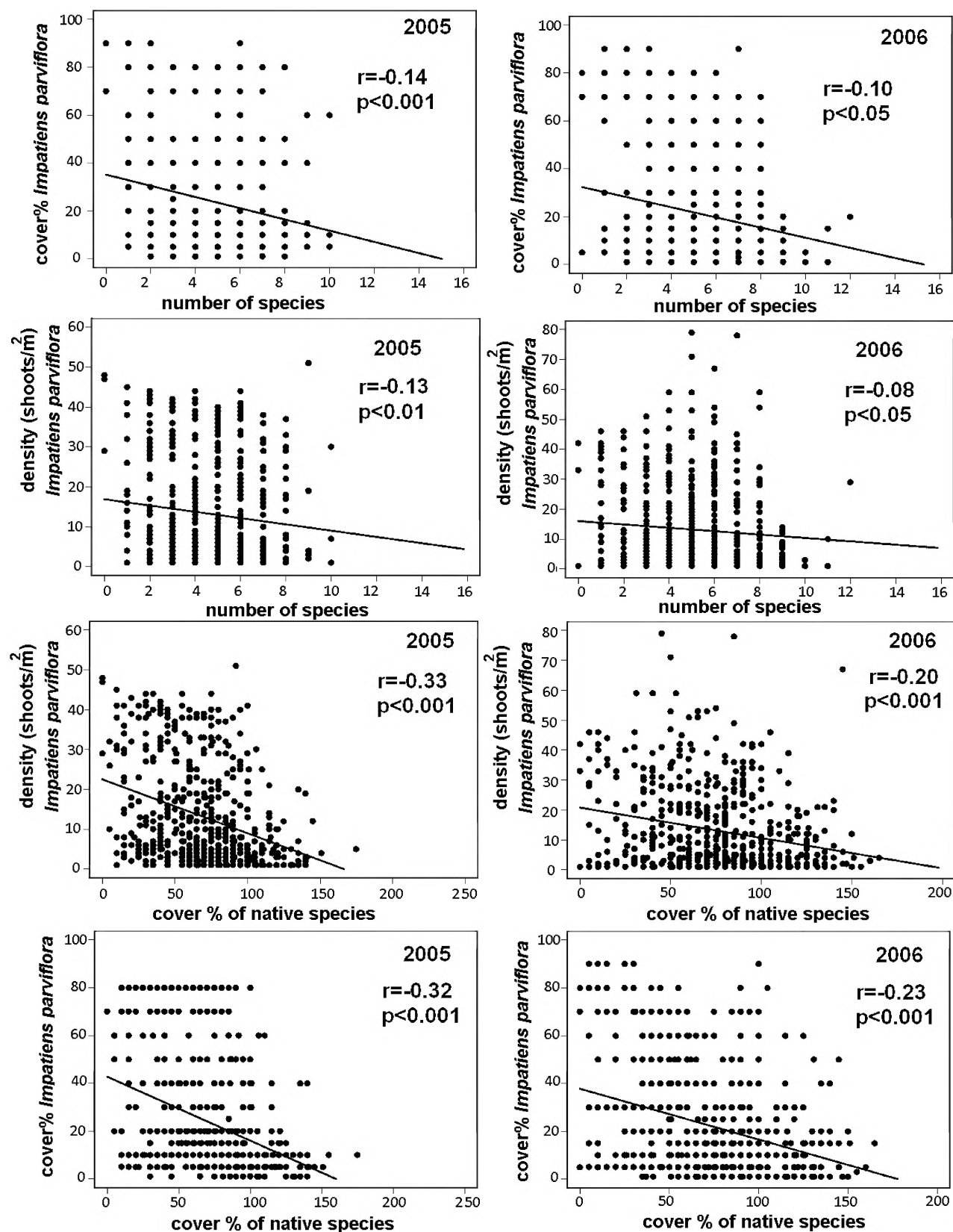
Fig. 53. Comparison of the association between the cover of *I. parviflora* and the cover of native species between the years in the Jurassic Upland (data for 10 study plots)

In the work by Chmura and Sierka (2006a), the patches of the same forest communities from two regions were pooled and subjected to statistical analysis. An analysis across the region obtained biased patterns. As is shown in Figure 52, the correlation for the forests of the Jurassic Upland is negative whereas for the Silesian Upland it is slightly positive. Such a divergence may be a consequence of the impact of extrinsic factors that permit small balsam and other components of ground flora to use disturbance sites on the forest floor together, thus there is a higher number of native species in the case of the Silesian Upland. For instance, a significant and positive correlation with the cover of herbaceous species was revealed for native but expansive presence of *Calamagrostis epigejos* in the forests of the region (Sierka, Chmura 2005). As regards small balsam, the only case in which there was also a positive correlation with the cover of the herb layer was the Sonian Forest in Belgium. The forest complex was built mainly by *Fagus sylvatica* and coniferous trees occupy ca. 8%. Perhaps a key reason is a disturbance of that area that is manifested by the massive occurrence of *I. parviflora*, which was stressed by Godefroid and Koedam (2010).

Obidziński and Symonides (2000) showed that the relationship, between density of *I. parviflora* and cover of other herbaceous species, which is expressed as a higher value of the correlation coefficient, was higher in the following year (1998) than in the previous one (1997). There was an opposite result for the number of native species. The values of both correlations analyses were similar and they are probably meaningless. In the present work when 2006 was compared with 2005, lower values for the correlation coefficients between density, the cover of small balsam and number and cover of native species were obtained. This might have resulted from a decrease in the biocenotic resistance of the LTR plots that were studied that were due to frequent trampling, which enhanced the explosion of the fruits and the seed dispersal of the plants owing to their penetration within the study plots. In the following years, the methods were modified in order to eliminate the effect of disturbances that were associated with performing the research, which could have contributed to the higher occurrence of small balsam within the LTR plots.

The effect of scale on relations with native species
Analysis of flora

In total 68 study plots were analyzed in terms of the accompanying flora and the frequency and cover of accompanying species. These study plots were situated in seven forest communities that represent oak-hornbeam forests *Tilio-Carpinetum* – TC (26 plots), swamp alder forests *Ribeso nigri-Alnetum* – RA (2), mixed coniferous forests *Querco roboris-Pinetum* – QP (19), acidophilous beech forests *Luzulo pilosae-Fagetum* – LF (7), thermophilous beech forests *Carici-Fagetum* – CF

(2), beechwood forests *Dentario glanduloase-Fagetum* – DF (9) and floodplain forests of *Alno-Ulmion* alliance – AU (3).
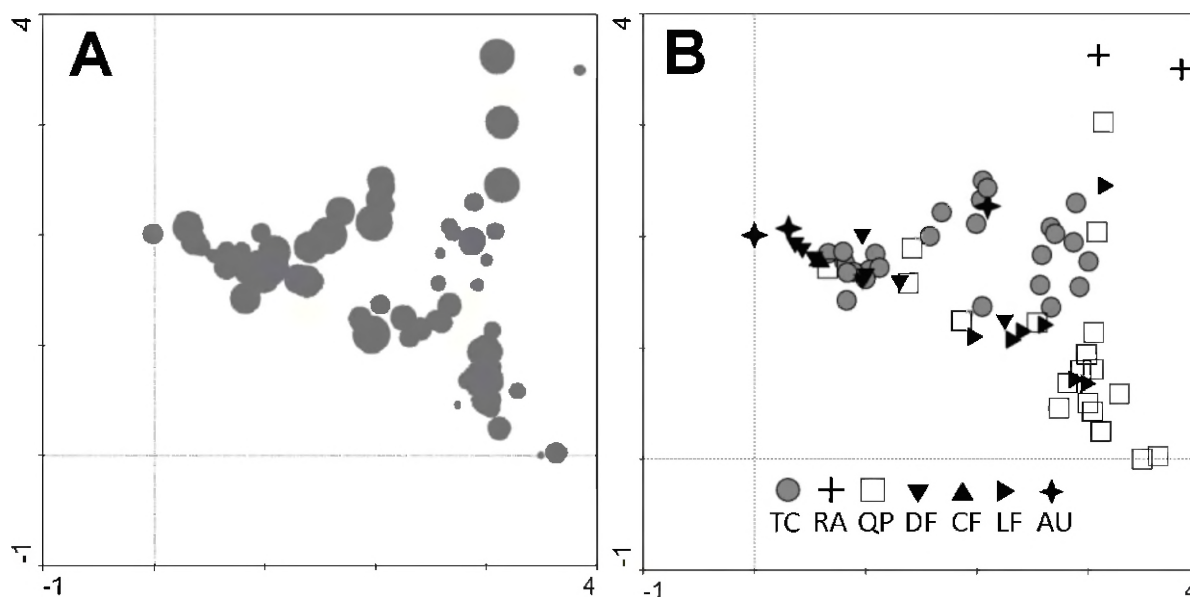
Fig. 54. Abundance of *Impatiens parviflora* and the distribution of the study plots that represent the various forest communities along the two first DCA axes in the Silesian-Krakow Upland. Abbreviations of plant communities see text.

These plots are diversified in regard to the abundance of *I. parviflora* (Fig. 54A). DCA, which was based on the sum of the covers of particular species on subplots within the study plots, produced four axes with eigenvalues 0.556, 0.400, 0.229, 0.202 and the length of gradients 3.840, 3.625, 2.463, 3.003. Their cumulative explained variation is 19.4%. At the level of the study plots, *I. parviflora* is not a significant variable in explaining species variation (Monte Carlo test CCA, p=0.309) based on their frequency (number of subplots occupied), whereas based on the sum of their covers, it is significant (p=0.015) although the inflation factor is too high because it was correlated with the other species that were present. Moreover, it explained only 2.3% of the variation in native species.

There were 191 species on the study plots but in 3628 subplots of 1m^2 with the presence of *I. parviflora*, there were 171 species while 173 species occurred in 3172 subplots without *I. parviflora*. In total 152 species were common for both types of subplots.

The participation of Grime's life strategies was very similar in both groups – plots with and without *I. parviflora* (Fig. 55).

The C-S stress tolerant competitors dominated (23.7%-22.8%) followed by C-S-R strategists (15.8-16.4%) and competitive ruderals (10.5%-11.5%). Representatives of two strategies were not found – SR – stress tolerant ruderals and S/SR strategists.

The distribution of Raunkiaer's life forms was as follows (Fig. 56): hemicryptophytes were the dominant group (44.8%-46.6%) of the total flora; geophytes (19.4%-19.0%), megaphanerophytes (12.1%-12.3%) and nanophanerophytes (11.5%-11.7%). The remaining groups played minor roles.

Anemochores were predominant among the accompanying species on subplots with *I. parviflora* – 41.4% and on subplots without – 40.2% (Fig. 55). Endozochores were the second most abundant group constituting 17.7% and 17.8% of flora, respectively.
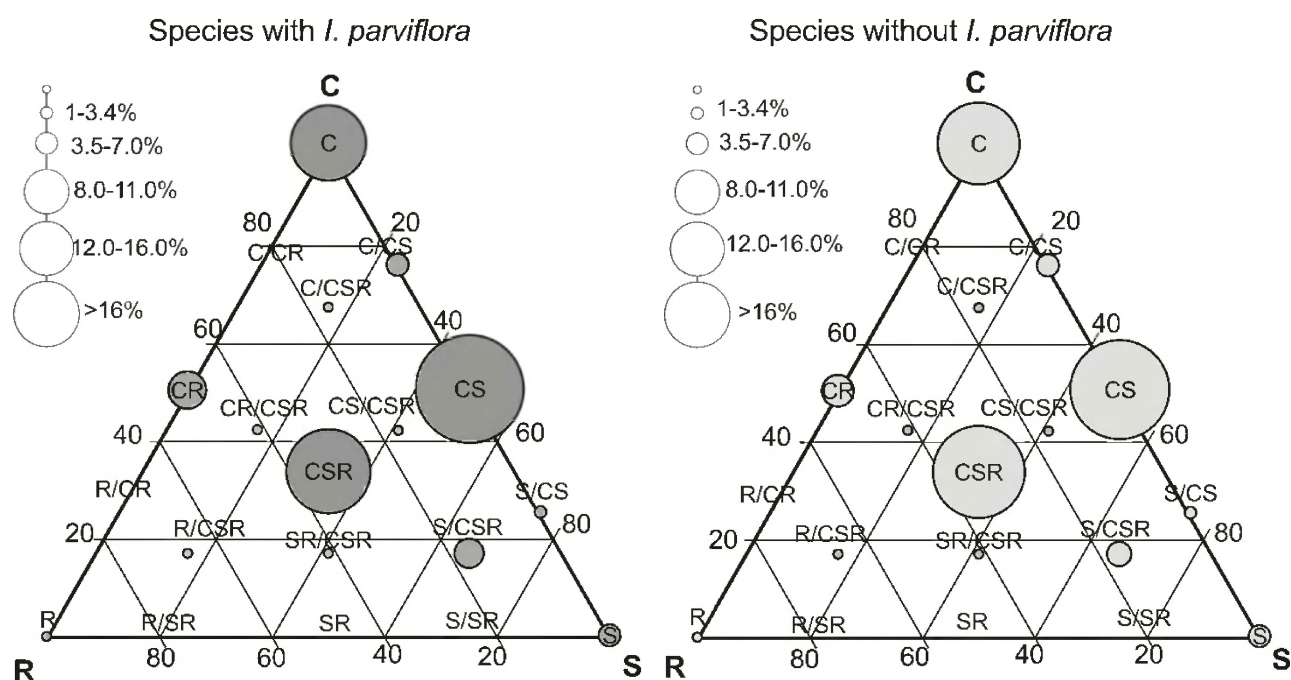
Fig. 55. Grime's C-S-R triangle for the accompanying flora of *Impatiens parviflora* on the sites with a presence (invaded) and on sites with an absence of the species (uninvaded)

Myrmecochores contributed 12.8% and 11.8%, respectively. The least abundant were hydrochores and autochores, which did not exceed 3.7% of the flora of the two groups of species (Fig. 57).

The distribution of the species that represent particular Ellenberg indicator values was similar in both groups of plants. With regard to light (L), the plants of the L6 and L7 values predominate, i.e. plants that prefer semi-shade and well-lit places but that can also tolerate partial shade. They both constitute 33.7% and 34.7% of the flora, respectively, for subplots both with and without *I. parviflora*. Plants that prefer shade and semi-shade conditions were quite numerous (L = 3 and L = 4) (Fig. 58 L).

Taking into account temperature (T) species of the T5 value dominate in both groups of plants reaching 46.3% and 46.9%, followed by species of the T6 value (24.5% and 26.9%) (Fig.

58T). Edaphic conditions, which were characterized by flora on sites with and without *I. parviflora*, showed the same trend. In regard to moisture (F), representatives of mesophytic habitats and fresh soils were the dominant groups on sites with or without small balsam (F= 5: 39.0% and 38.7%). Moreover, species that prefer a slightly moist substratum were numerous (21.3% and 19.1%) (Fig 59F). The intermediate and slightly acid or weakly alkaline soils indicators dominate in both groups of plants, i.e. values 6-7 contributed 19.5%, 20.2% and 29.6% and 28.3%, respectively. The species that are indicators of calcium carbonate constituted 10.6% and 10.4% of both floras (Fig. 59R). Among the introgen indicator species plants that occur in intermediate-rich mineral nitrogen compounds were the most numerous (19.5% and 20%).
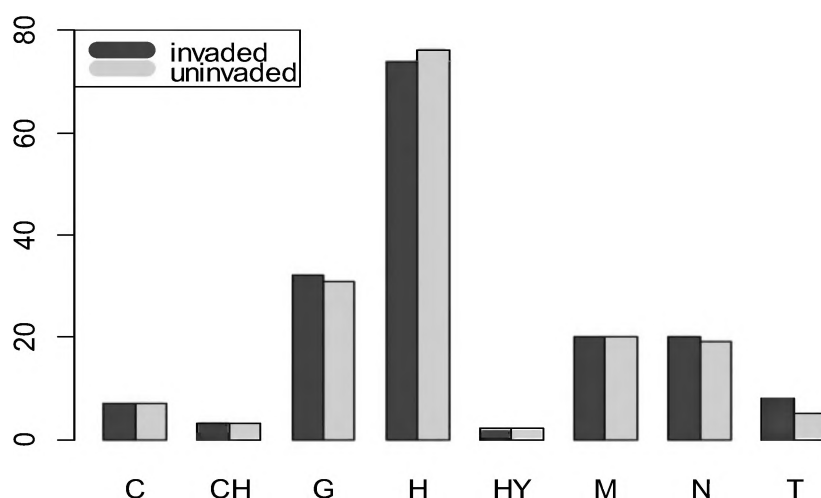
Fig. 56. Distribution of Raunkiaer's life forms of the accompanying flora of *Impatiens parviflora* on sites with a presence (invaded) and sites with an absence of the species (uninvaded). Abbreviations: C – chamaephytes, CH – herb chamaephytes, H – hemicryptophytes, HY – hydrophytes, G – geophytes, N – nanophanerophytes, M – megaphanerophytes, T – therophytes
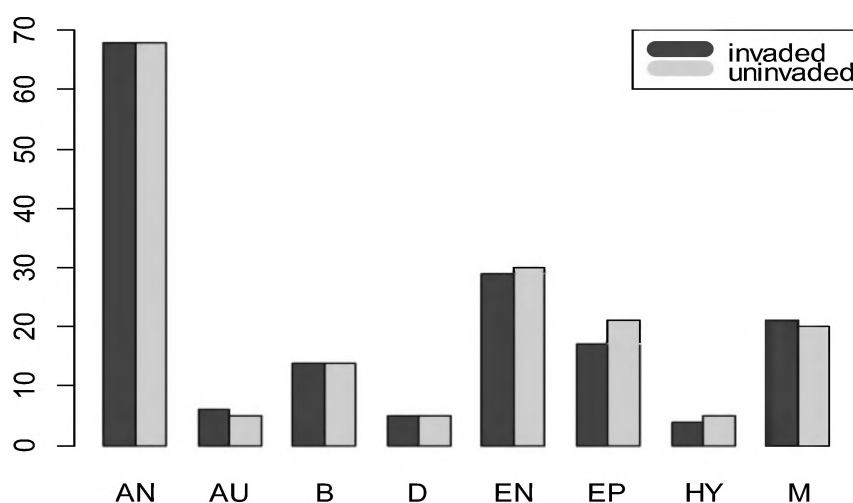
Fig. 57. Distribution of the types of the dispersal modes of the accompanying flora of *Impatiens parviflora* on sites with a presence and on sites with an absence of the species. AN – anemochores, AU – autochores, B – barochores, D – dyszoochores, EN – endozochores, EP – epizochores, HY – hydrochores, M – myrmecochores

The plants that tend to occurr in nitrogen-rich soils (values 6 and 7) are also a major part of both floras (Fig. 59N).
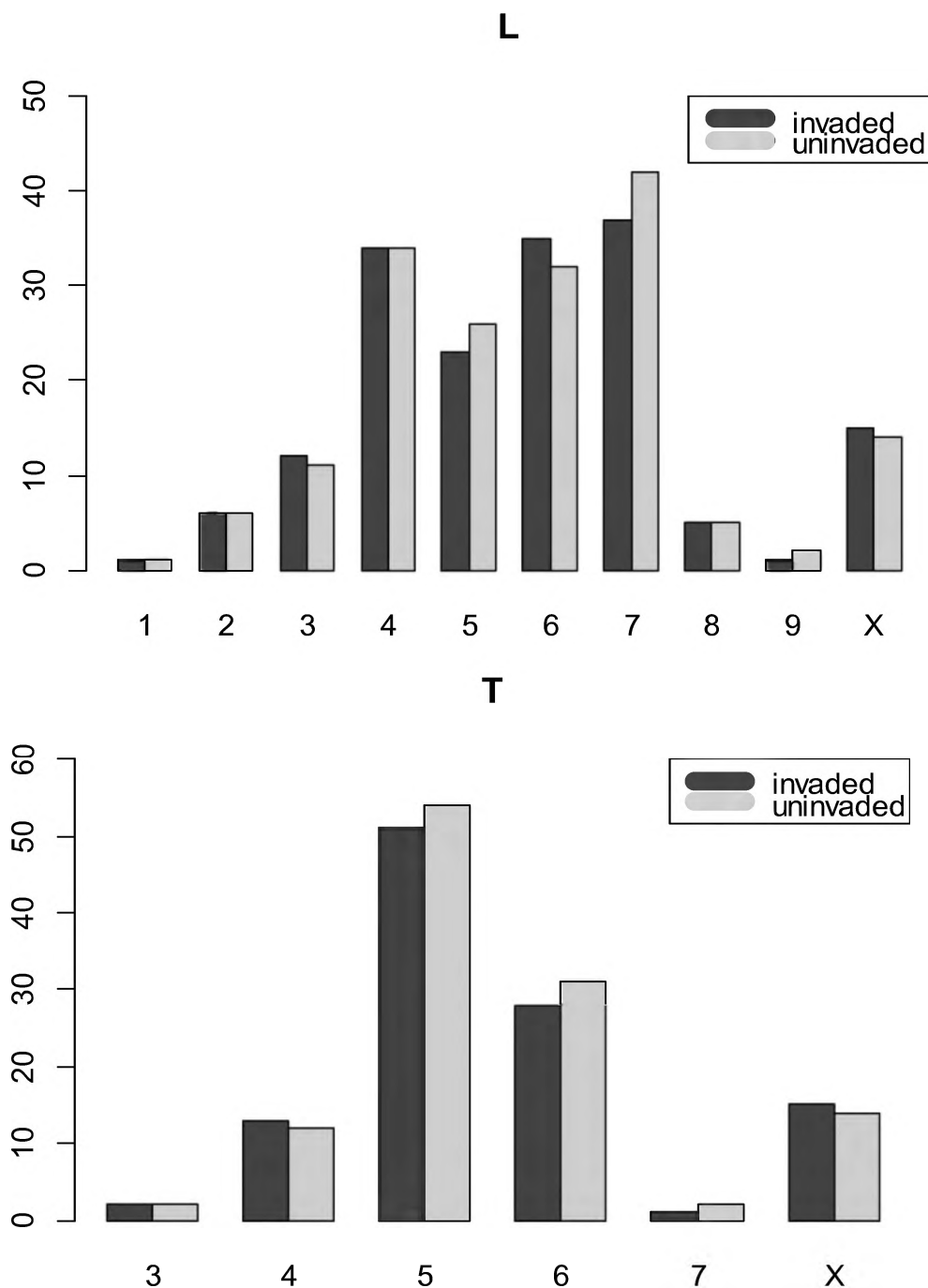
Fig. 58. Distribution of representatives of particular Ellenberg values for the climatic conditions (L–light, T–temperature) of the accompanying flora of *Impatiens parviflora* on sites with a presence and on sites with an absence of the species
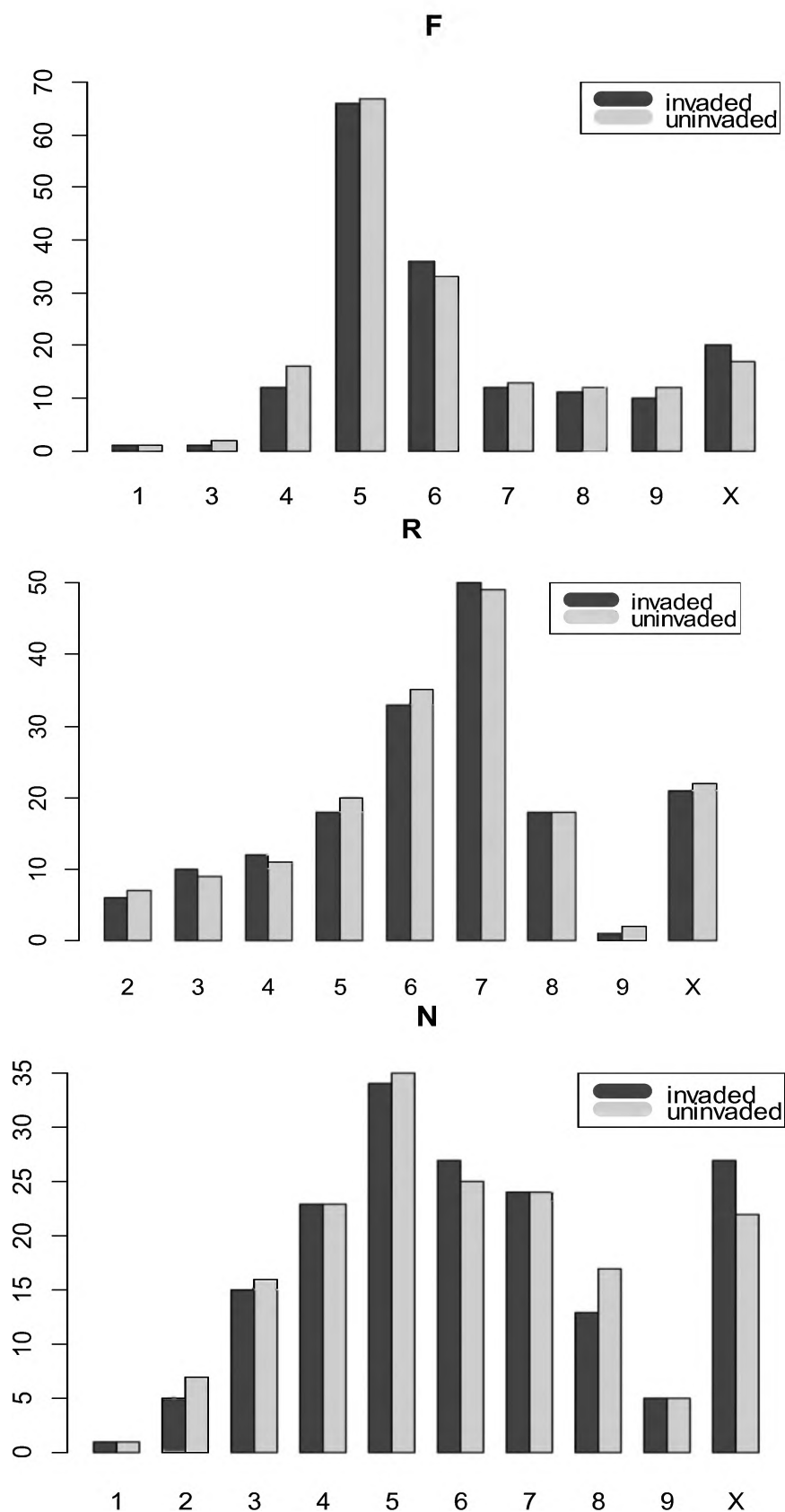
Fig. 59. Distribution of representatives of particular Ellenberg values for the edaphic conditions (F – humidity, R – soil reaction, N – nitrogen) of the accompanying flora of *Impatiens parviflora* on sites with a presence and sites with an absence of the species

Analysis of differences in plant functional types of accompanying species on a large scale

There were no significant differences in the mean total number of occurrences between the species that were present on all of the invaded subplots and all of the uninvaded subplots in terms of life forms, dispersal mode or Grime's strategies (data not shown). Moreover, the mean cover of plant functional types did not differ significantly between all of the invaded and uninvaded subplots combined (Tab. 26).

Tab. 26. Comparison of the mean cover of accompanying species on sites with (invaded) or without *Impatiens parviflora* (uninvaded) within a 100 m^2 area based on 68 permanent plots.

	Invaded	Uninvaded	Statistics, probability
Life form:			
Chamaephytes	10.68±15.25	12.26±22.53	W = 2370, p = 0.7884
Herb chamephytes	5.15±12.90	3.94±11.07	W = 2364, p = 0.7916
Geophytes	52.60±38.82	53.07±45.42	W = 2379.5, p = 0.7706
Hemicryptophytes	62.09±71.53	52.37±60.82	W = 2448.5, p = 0.5538
Hydrophytes	0.13±1.09	0.06±0.29	W = 2245.5, p = 0.3264
Megaphanerophytes	28.56±32.45	27.60±32.59	W = 2409.5, p = 0.6728
Nanophanerophytes	14.59±18.26	12.85±14.29	W = 2354, p = 0.8557
Therophytes	7.13±16.27	3.15±8.83	W = 2482.5, p = 0.3919
Dispersai mode:			
Anemochores	44.59±38.31	42.13±36.06	W = 2415.5, p = 0.6539
Autochores	19.63±23.65	16.65±18.40	W = 2394.5, p = 0.7193
Barochores	16.25±20.54	14.75±17.65	W = 2377, p = 0.7783
Dyszoochores	12.26±17.45	8.57±11.62	W = 2499, p = 0.4122
Endozoochores	28.76±36.04	27.01±22.70	W = 2171, p = 0.5407
Epizoochores	23.35±36.22	18.18±28.19	W = 2371, p = 0.7975
Hydrochores	0.79±4.51	1.96±15.27	W = 2248.5, p = 0.5013
Myrmecochores	35.22±43.47	36.06±59.24	W = 2452.5, p = 0.5393
Grime strategy:			
Competitors	27.31±31.35	27.74±33.36	W = 2294, p = 0.9393
Stress tolerators	13.03±19.17	12.06±16.04	W = 2319, p = 0.9766
Ruderals	2.34±6.76	1.44±5.14	W = 2338.5, p = 0.8776
Competitive ruderals	17.56±29.71	13.07±19.10	W = 2390.5, p = 0.7272
Stress tolerant competitors	56.21±50.75	55.07±57.91	W = 2451.5, p = 0.5451
CSR strategists	62.87±59.09	54.13±55.06	W = 2529.5, p = 0.3448

Analysis of differences in plant functional types of accompanying species on a small scale

The invaded subplots had a lower mean cover of chamaephytes (Fig. 60C) and geophytes (Fig 60G), whereas therophytes had a higher mean cover (Fig 60T).

Fig. 60. Comparison of the mean cover of Raunkiaer life forms representatives within accompanying species among 1 m^2 plots with and without *Impatiens parviflora*. C – chamaephytes, CH – herb chamaephytes, H – hemicryptophytes, HY – hydrophytes, G – geophytes, M – megaphanerophytes

N   NS   **T   p<0.001**

Fig. 60. continued. Comparison of mean cover of Raunkiaer life forms representatives within accompanying species between 1 m 2 plots with and without *Impatiens parviflora*. N – nanophanerophytes, T – therophytes, NS – nonsignificant

Competitors had a lower cover on invaded plots than on uninvaded (Fig. 61C), whereas ruderals had a much higher (almost twofold) cover on invaded subplots (Fig. 61R). The mean cover of competitive ruderals was a little higher on invaded subplots than on uninvaded ones (Fig 61CR). In turn, stress tolerant competitors had a higher mean cover on uninvaded subplots (Fig 61CS).

On average, anemochores had a higher cover on uninvaded subplots (Fig. 62A) as did endozochores (Fig. 62EN). Invaded plots had a significantly higher mean cover of dyszoochores and epizoochores (Fig. 62D,EP). Myrmecochores reached a higher mean cover on subplots without *Impatiens parviflora*.

The relationship between the abundance of small balsam and the cover of species representing plant functional groups was also affected by scale (Tab. 27). When the frequencies of a species were taken into account, only two groups significantly correlated, i.e. the cover of chamaephytes (negative correlation) and the cover of therophytes and anemochores (positive correlation). At the scale of $1m^2$ there were many significant relationships but they are very weak (Tab. 27). A comparison of the correlation coefficients for anemochores led to contradictory results. At the lower scale, the correlation was very weak and negative but at the large scale – medium and positive.
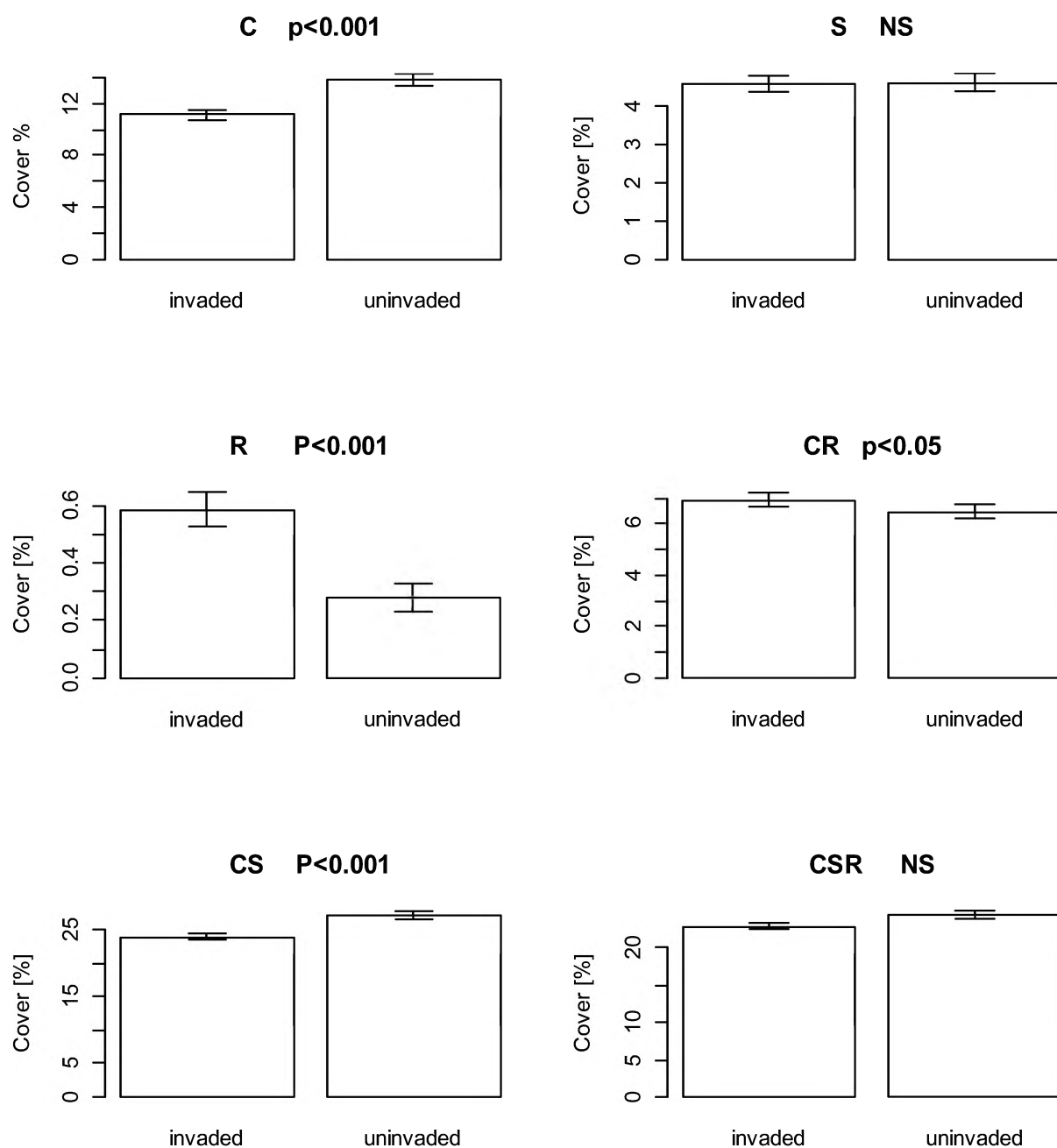
Fig. 61. Comparison of the mean cover of representatives of Grime strategies within the accompanying species among 1 m^2 plots with and without *Impatiens parviflora*. Explanations: C – competitors, S – stress tolerators, R – ruderals, CR – competitive ruderals, CS – stress tolerant competitors, CSR – CSR strategists, NS – nonsignificant
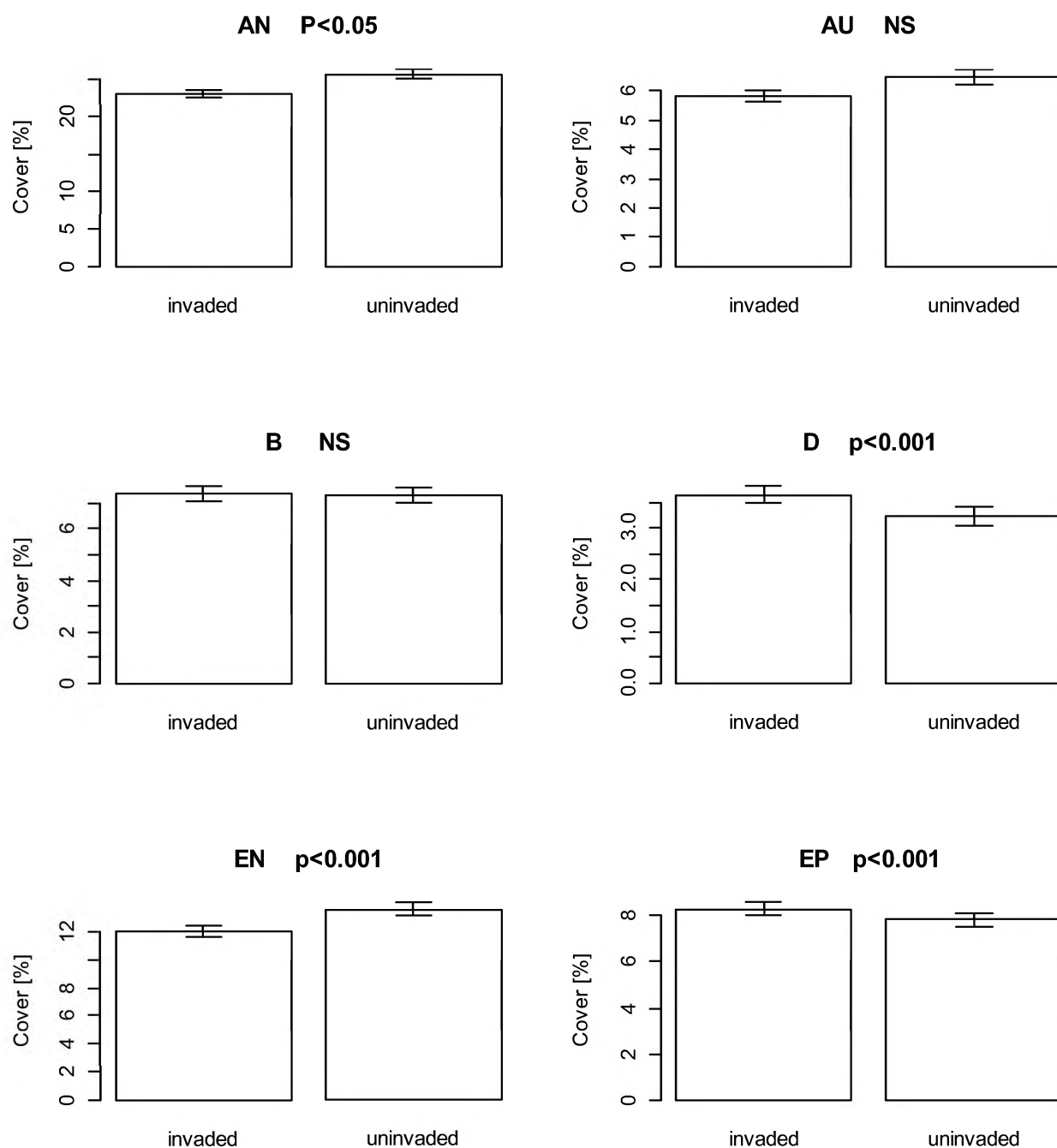
Fig. 62. Comparison of the mean cover of dispersal mode representatives within accompanying species among 1 m² plots with and without *Impatiens parviflora*. Explanations: AN – anemochores, AU – autochores, B – barochores, D – dyszoochores, EN – endozochores, EP – epizochores, NS – nonsignificant

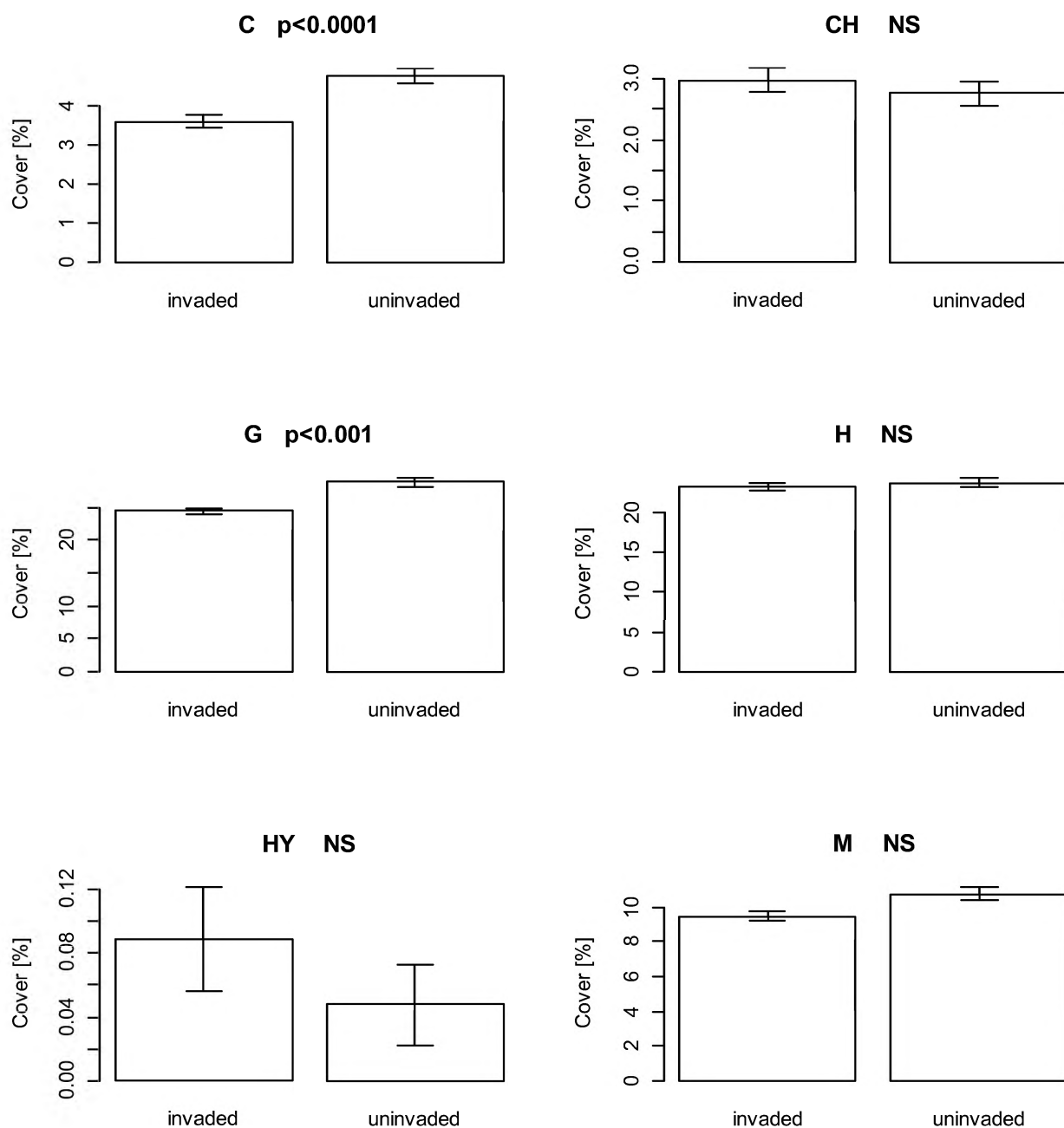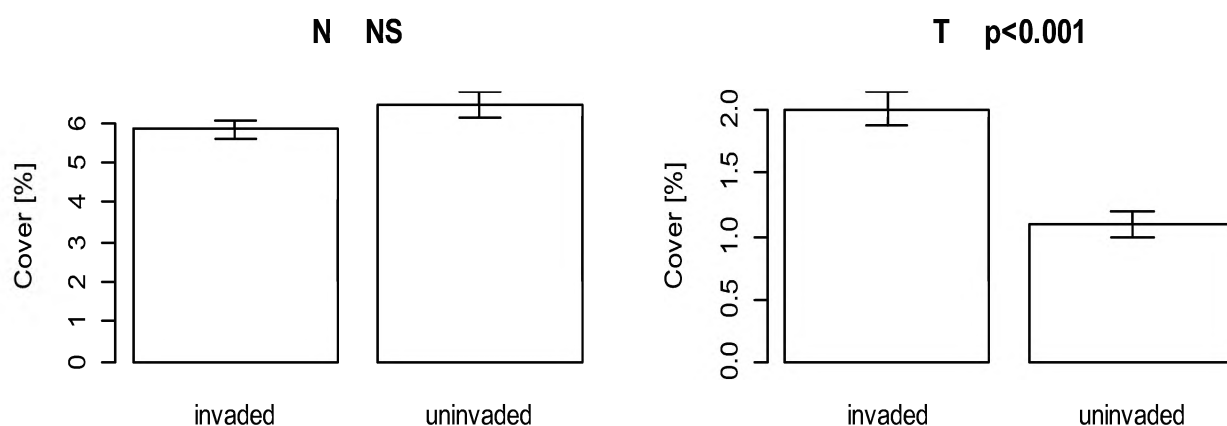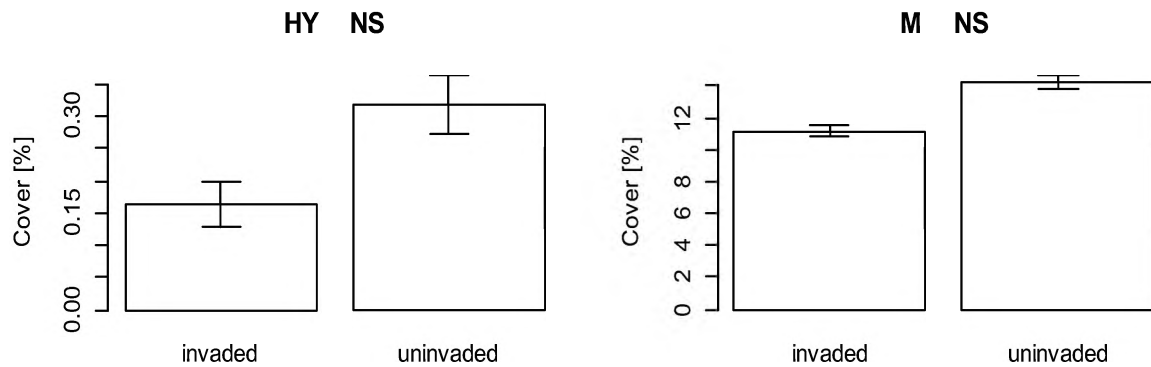Fig. 62. continued. Comparison of the mean cover of dispersal mode representatives within accompanying species among 1 m² plots with and without *Impatiens parviflora*. Explanations: HY – hydrochores, M – myrmecochores, NS – nonsignificant

Some studies have shown that a relationship exists between the species cover of native and non-native species and their covers: positive at the landscape scale (e.g., Stohlgren *et al*. 1999; Sax 2002), a vegetation scale lower that 100 m² and negative at scales of < 1 m² (neighborhood scales). Thus, it can be expected that when comparing flora, the frequency and cover of native species among invaded and uninvaded plots were also affected by the scale. There were no significant differences in accompanying flora from all of the invaded and uninvaded subplots that were pooled. The total flora from 68 100 m² study plots was comparable to the flora at the landscape level. The majority of studies have shown that at large areas > 1000 m² and at vegetation scales as well – 100 m² (Stohlgren *et al*. 1999, 2003, 2006), there is a strong positive relationship between native species richness and the cover, biomass and relative cover of alien plant species. At lower scales – subplot (1m²), the differences in particular functional groups (life strategy, dispersal mode, life form) show which sites are preferred by small balsam. Perennial plants (geophytes, chamaephytes), competitors, stress-tolerant competitors, myrmecochores, anemochorous and endozoochorous plants are more abundant on uninvaded plots, which may indicate overcompetition by these species. Native annual plants (therophytes, ruderals) indicate a disturbance on microsites where small balsam grows. It is more difficult to explain the higher cover of dyszoochorous (tree seedlings) and epizoochorous plants on invaded plots. Small balsam tolerates a high, but not too abundant, cover of tree seedlings due to its small aboveground biomass and shallow root system. Such places are avoided by other herbaceous plants but are used by *I. parviflora*.

The relationship between the cover and the total cover of the groups that had been distinguished is modified by scale. A significant negative or positive correlation between the invasive species and

cover of particular functional groups at the scale of 100 m^2 was demonstrated by Chmura (2013) for red oak *Quercus rubra*. In the present study at the same scale, only two correlations turned out to be significant, whereas at a lower scale the majority were significant but they were very weak and unimportant. This proves that small balsam when compared to other species plays an insignificant role in interspecific relations. If a species has an impact on coexisting plants, it could be expected that not only on some species as such but in general plant traits or plant functional groups are affected.

Tab. 27. Relationships (Spearman rank test) between the cover of particular functional groups and the abundance of *I. parviflora*

	Scale of subplot [1m^2]		Scale of plot [100 m^2]	
Life form:	rs	p	rs	p
Chamaephytes	-0.0585	<.0001	-0.3510	0.0033
Herb chamaephytes	0.0523	<.0001	ns	
Geophytes	-0.1148	<.0001	ns	
Hemicryptophytes	ns		ns	
Hydrophytes	0.0340	0.0050	ns	
Megaphanerophytes	-0.0293	0.0155	ns	
Nanophanerophytes	ns	0.2688	ns	
Therophytes	0.0864	<.0001	0.3127	0.0094
Dispersal mode:				
Anemochores	-0.0334	0.0059	0.2442	0.0448
Autochores	-0.0524	<.0001	ns	
Barochores	-0.0259	0.0330	ns	
Dyszoochores	0.0492	<.0001	ns	
Endozoochores	ns		ns	
Epizoochores	ns		ns	
Hydrochores	-0.0478	<.0001	ns	
Myrmecochores	-0.1009	<.0001	ns	
Grime strategy:				
Competitors	-0.0585	<.0001	ns	
Stress tolerators	-0.0428	0.0004	ns	
Ruderals	ns		ns	
Competitive ruderals	ns		ns	
Stress tolerant competitors	-0.0280	0.0210	ns	
CSR strategists	-0.0758	<.0001	ns	

3.3.4. Ecological conditions of the occurrence of mycorrhiza

The history of the evolution of the views on mycorrhiza in *I. parviflora* was described in detail in a previous work (Chmura, Gucwa-Przepióra 2012). A detailed list of samples of the data on the presence/absence of AM is presented in Table 28.

As a reminder, one can first say that the report indicates that there were no mycorrhiza in this species and that recently, the species is definitely mycorrhizal (Štajerová *et al.*, 2009). An arbuscule structure was found in each AM+ sample (Fig. 63). Moreover, other structures such as vesicles were observed in seven cases and a coil only once (Tab. 29). The mycorrhiza structures that were found in *I. parviflora* are typical for the arbuscular type (Fig. 64). There are significant difference in the frequency of AM+ plants of *Impatiens parviflora* among forest communities (G = 11.03, p = 0.011). AM+ plants were encountered most frequently in oak-hornbeam patches and they were rarest in mixed coniferous forests (Fig. 63).

Tab. 28. The number of samples per site and the forest type in the study area. The number of samples where AM+ plants were found are shown in parentheses (Chmura, Gucwa-Przepióra 2012, supplemented)

Nature reserve	Forest type				Total
	FA	DF	TC	QP	
Bukowica (50°04'43''N, 19°23'55''E).		3(1)		2	5
Dolina Eliaszowki (50°10'18''N, 19°38'02''E).			1(1)	2	3
Dolina Kluczwody (50°09'54''N, 19°49'10''E).	2(2)		1(1)	1	4
Dolina Racławki (50°09'49''N, 19°41'33''E).	3(3)	1(1)			4
Lipowiec (50°04'42''N, 19°26'38''E).		2	3(3)	1(1)	6
Skała Kmity (50°06'06''N, 19°48'38''E).		2(2)	2(2)		4
Wąwóz Bolechowicki (50°09'30''N, 19°46'55''E).	3	1(1)			4
Total	8	9	7	6	30

Some samples were characterized by maximum values of mycorrhiza colonization such as *F%* – 100% and (*a%*) – arbuscule richness in root fragments where arbuscules were present – 94 (Tab. 30). These samples originated from floodplain forests. The sites where AM+ plants were encountered were characterized by a higher concentration of magnesium and higher values of soil reaction (Chmura, Gucwa-Przepióra 2012, Tab. 31).

Tab. 29. Presence of mycorrhiza structure in particular samples

No sample	arbuscules	vesicles	coils	code of forest community
1	x			FA
2	x			FA
3	x			FA
4	x			DF
5	x			DF
6	x	x	x	FA
7	x	x		FA
8	x			TC
9	x	x		TC
10	x			TC
11	x			TC
12	x			TC
13	x	x		DF
14	x	x		TC
15	x			DF
16	x	x		DF
17	x	x		QP
18	x			TC

DF – beechwood forests *Dentario glandulosae-Fagetum*, TC – oak hornbeam forests *Tilio-Carpinetum*, FA – alder forests *Fraxino-Alnetum*, QP – mixed coniferous forests *Querco roboris-Pinetum*
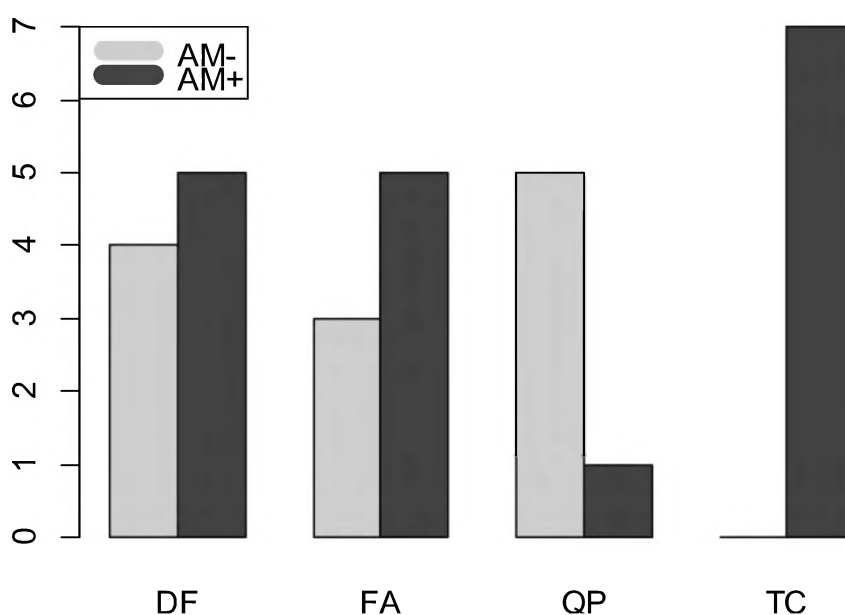
Fig. 63. Frequency of the presence of arbuscular mycorrhiza in *Impatiens parviflora* in the forest communities that had been distinguished. Explanations: DF – beechwood forests *Dentario glandulosae-Fagetum*, FA – alder forests *Fraxino-Alnetum*, QP – mixed coniferous forests *Querco roboris-Pinetum*, TC – oak hornbeam forests *Tilio-Carpinetum*

The AM+ from floodplain forests *Fraxino-Alnetum* were typified by higher values of all of the mycorrhization indices in comparison with the three remaining forest communities. The lowest values were observed in fertile beech forests (Tab. 32 after Chmura, Gucwa-Przepióra 2012).
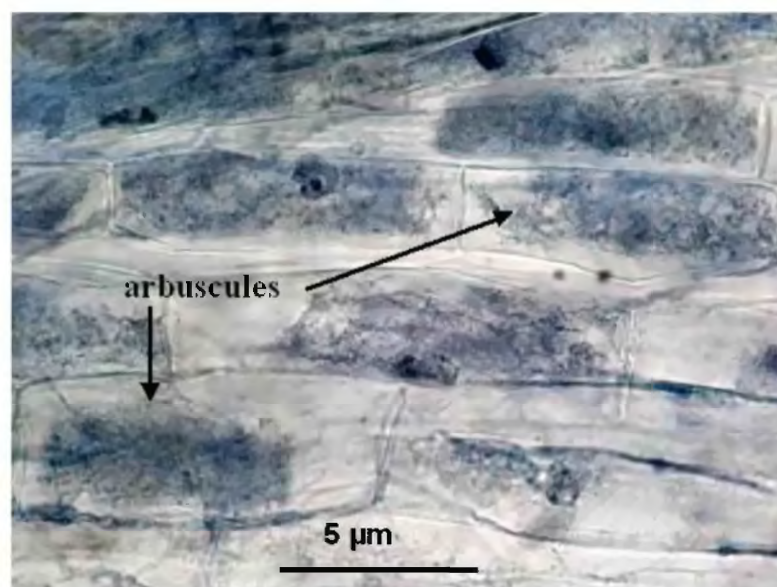
Fig. 64. Presence of arbuscules in roots of *Impatiens parviflora* (photo by Gucwa-Przepióra)

Tab. 30. Descriptive statistics of arbuscular mycorrhization indices

	F	M	m	a	A
Mean	57.51	28.03	39.93	68.20	22.01
SD	29.86	23.27	25.31	19.17	20.84
min	3.33	0.16	3.4	26.47	0.08
max	100	76.33	76.33	94.44	68.5

Tab. 31. Differences in the soil properties of samples from forests where mycorrhizal individuals (AM+) and non-mycorrhizal individuals of *I. parviflora* were present (after Chmura, Gucwa-Przepióra 2012, modified)

Soil parameter	AM+	AM-	P
pH	5.9±1.5	4.7±1.6	*
pH_{KCL}	5.4±1.6	4.2±1.6	*
C	4.9±2.9	5.0±2.3	ns
Loss on ignition (%)	12.0±5.6	12.0±3.3	ns
N_T	0.3±0.1	0.4±0.3	ns
C:N	15.6±3.5	16.6±5.5	ns
P (mg/100 g)	3.0±2.9	8.2±16.1	ns
Mg (mg/100 g)	6.7±9.2	2.5±3.8	*
K (mg/100 g)	6.0±5.5	4.7±2.5	ns
Ca (mg/100 g)	422.0±265.2	341.2±461.4	ns
Na (mg/100 g)	3.1±0.7	3.5±0.7	ns
$CaCO_3$ (mg/100 g)	1.5±3.8	1.9±5.7	ns

Tab. 32. Comparison of mycorrhiza colonization parameters (Mean±SE) between studied forest communities (after Chmura, Gucwa-Przepióra 2012, modified)

	F	M	m	a	A
AU	66.8±4.5a	34.7±3.5a	40.1±3.4a	74.9±3.9a	30.0±3.1a
DF	13.3±2.9c	6.4±1.6c	16.4±4.1c	19.5±4.2c	3.9±1.0c
TC	35.7±5.0b	13.9±2.9b	21.1±3.4b	45.7±3.7b	9.6±2.2b
QP	21.9±5.8b	11.9±3.6b	17.1±4.8c	22.2±6.0c	8.9±2.9b

DF – beechwood forests *Dentario glandulosae-Fagetum*, TC – oak hornbeam forests *Tilio-Carpinetum*, FA – alder forests *Fraxino-Alnetum*, QP – mixed coniferous forests *Querco roboris-Pinetum*

The main difference between the present study and the work by Chmura and Gucwa-Przepióra (2012) is related to the analysis of data that was obtained. A restricted analysis or choice of method of analysis can cause the loss of some data and an underestimation of the results. Using the new *F%* approach seems to be a more explanatory variable to explain the vegetative and generative attributes of plants. It explains the number of flowers and fruits and some leaf morphology traits better. The remaining AM indices were positively correlated with the height of plant, whereas in the original study (Chmura, Gucwa-Przepióra 2012) index *a%* and *m%* did not correlate with any of the morphometric attributes (Tab. 33).

Obviously, morphometric variables are correlated with each other. The taller the plant, the higher the number of flowers and seeds (Coombe 1956). AM colonization indices were also correlated with each other. However, it is very interesting to what extent the results show a statistical artifact or causal associations. Can the presence of arbuscules or their quantity stimulate the development of flowers or seeding seeds? Does AM influence biomass allocation? The answers to these questions in the future in relation to invasive species can contribute to wider knowledge about plant invasions. A series of experiments with the inoculation of AM fungi under controlled conditions (laboratories, greenhouses) and the observation of life history traits or biomass allocation may be useful and help to solve some of the problems.

This study and the one done by Chmura and Gucwa-Przepióra (2012) demonstrated that a greater number and more fecund individuals of *I. parviflora* were characterized by higher values of the AM colonization indices. It was therefore inferred that AM may have caused the gregariousness and fecundity of the species. There is another possible explanation for this phenomenon. An opposite pattern is that taller and more fecund plants are colonized by AM fungi more frequently.

Tab. 33. Comparison of the Pearson and Spearman rank correlation coefficients between the soil variables and mean morphometric features of *I. parviflora* and mycorrhiza colonization (P<0.05), (after Chmura, Gucwa-Przepióra 2012, modified). The results between pooled AM colonization and morphometric features of individuals in the sample are shown in brackets.
(*F%*) – mycorrhizal frequency (*M%*) – relative mycorrhizal root length, (*m%*) – intensity of colonization within individual mycorrhizal roots, (*A%*) – relative arbuscular richness, (*a%*) – arbuscule richness in root fragments where arbuscules were present, ns – non-significant

Soil properties	Mycorrhizal parameters				
	F%	A%	a%	M%	m%
pH(H₂O)	0.56	ns	0.64	ns	ns
pH(KCL)	0.58	ns	0.65	ns	ns
C:N	-0.51	ns	-0.56	ns	ns
Ca (mg/100g)	ns	ns	0.51	ns	ns
Mean height of plants (height of a plant)	0.62(0.28)	0.77(0.21)	ns(0.32)	0.71(0.21)	ns(0.15)
Mean number of flowers (number of flowers)	ns(0.15)	0.74(ns)	ns(ns)	0.69(ns)	ns(ns)
Mean number of fruits (number of fruits per a plant)	ns(0.14)	0.76(ns)	ns(ns)	0.71(ns)	ns(ns)
Mean length of leave (length of leave per a plant)	ns(0.14)	0.66(ns)	ns(ns)	0.62(ns)	ns(ns)
Mean width of leaves (width of leave per a plant)	ns(0.15)	0.65(0.13)	ns(0.21)	0.62(0.12)	ns(ns)

All congeners within the genus *Impatiens* in Europe are not equally mycorrhizal plants. Himalayan balsam is considered to be sparsely colonized by the arbuscular mycorrhizal fungi AMF (Tanner, Gange 2013). Moreover, its presence in a community may affect AMF and decrease their percentage of colonization and as a consequence, this may lead to a decrease in the shoot biomass of native plants. However, mycorrhiza in this plant was not investigated in that study. In a previous work (Chmura, Gucwa-Przepióra 2012), the hypothesis was that when small balsam is colonized by AM fungi, it can be a beneficent of AM presence. There is no information about its impact on AMF in the soil. If Himalayan balsam affects microbial community, it is possible that role of *I. parviflora* in a plant community is similar. If small balsam, under favorable conditions, is more frequently colonized by AMF that other species in a community, this can indirectly have an impact on the remaining plant species that are present. Future research should focus on AMF in coexisting species on sites that have invaded and those that are uninvaded by *I. parviflora* in order to explain the role of arbuscular mycorrhiza in the invasiveness of the species.

Other fungi-like pathogenic fungi and dark septate endophytes (DSE) were absent in the samples that were investigated. DSE are sometimes reported to be present only in non-mycorrhizal plants and a negative correlation between AM and DSE fungal colonization has been observed (Chaundry *et al.* 2009; Muthukumar, Vediyappan 2010). Thus, it is possible that these fungi do not

colonize the roots of *I. parviflora*; however, further research should be conducted in order to solve this problem. This is important because parasitic ones are also known among the various symbiotic interactions of DSE with plants (Jumpponen 2001). The absence of pathogenic fungi and facultative pathogenic fungi in roots might also enhance the invasion success of small balsam. A reduced control by natural enemies in the introduced range compared with the native range, which is known as the enemy release hypothesis, is believed to be one of the important causes of alien plant species invasion (Colautti *et al.* 2004).

3.3.5. Interactions with coexisting plant species
Changes in species composition of plant communities invaded

A cluster analysis (CA) of the particular plots in the subsequent years based on the frequency of all of the species that were present on the study plots revealed different patterns of changes on the sites (Fig. 65). The vegetation data of native species was the most similar in the first two years on study plots 1, 3,4, 6, 7, 8 and 10 (Fig. 65A,C,D,F,G,H,I respectively), whereas on the other study plots – 2, 5 and 9, distant years occurred in the same clusters (Fig. 65B,E,J). It could have been expected that the successive years would have be close in common clusters or in the closest clusters. Assuming that time is the only factor that affects distance among the subsequent vegetation seasons, then a cluster analysis of study plot 1 would be a good example of such a phenomenon (Fig. 65A). There, the nearest years are grouped close to each other. All of the study plots from the initial invasion group and saturation invasion group were found in the first group in which the first two vegetation years were the most similar. The second group, which included study plots 2, 5 and 9, belongs to the intermediate invasion group. This group underwent the most significant changes in the population dynamics of small balsam, which could be reflected in the frequency and abundance of accompanying species.

There were significant differences in the total mean cover of native plants among the vegetation seasons on all of the study plots. Changes even occurred in two subsequent years on six of the study plots (3, 5-9) (Fig. 68, 70-74).
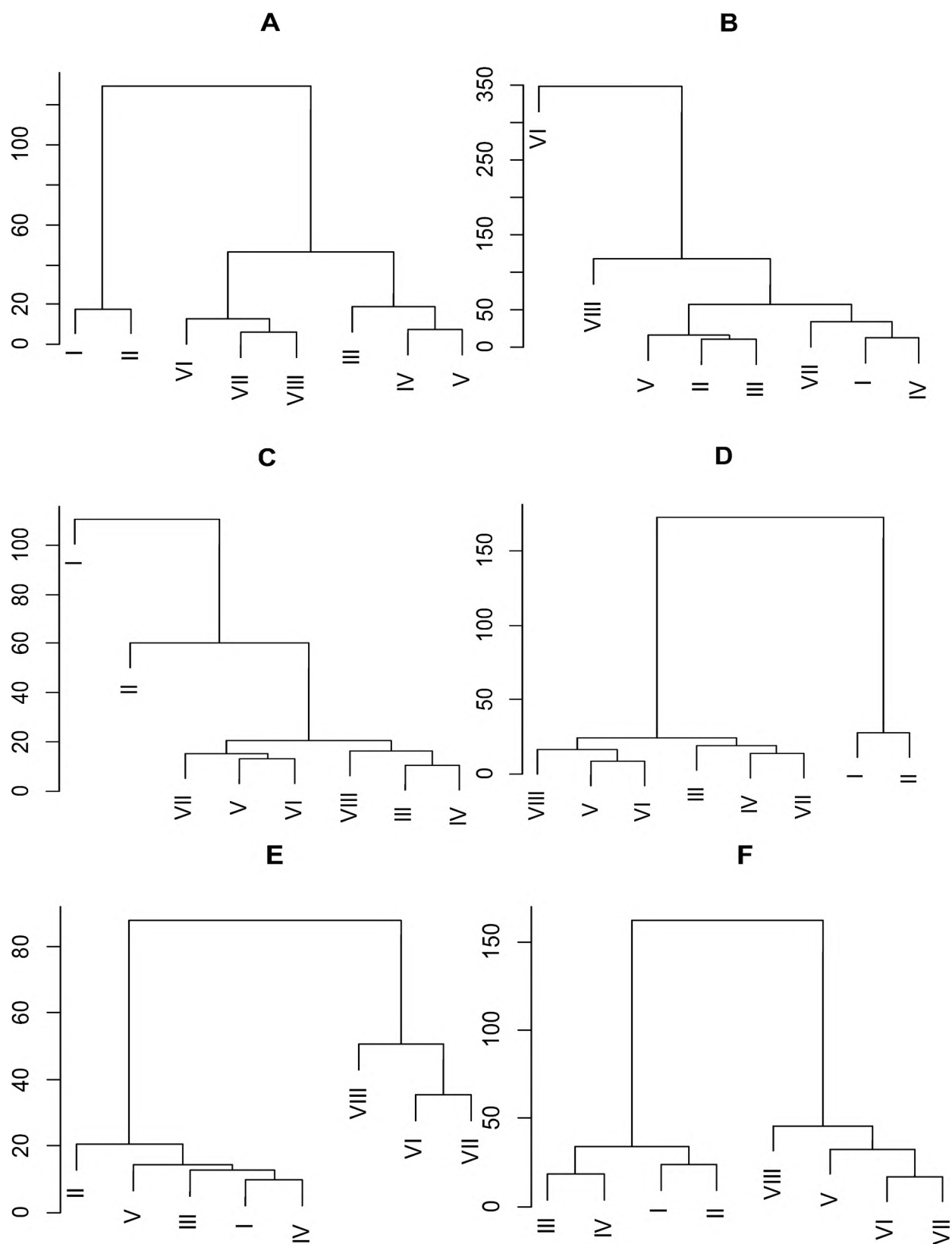
Fig. 65. Cluster analysis (Euclidean distance, Ward method) of successive stages of vegetation based on the total cover of species on study plots 1–6. Explanations: I – 2005…VIII – 2012
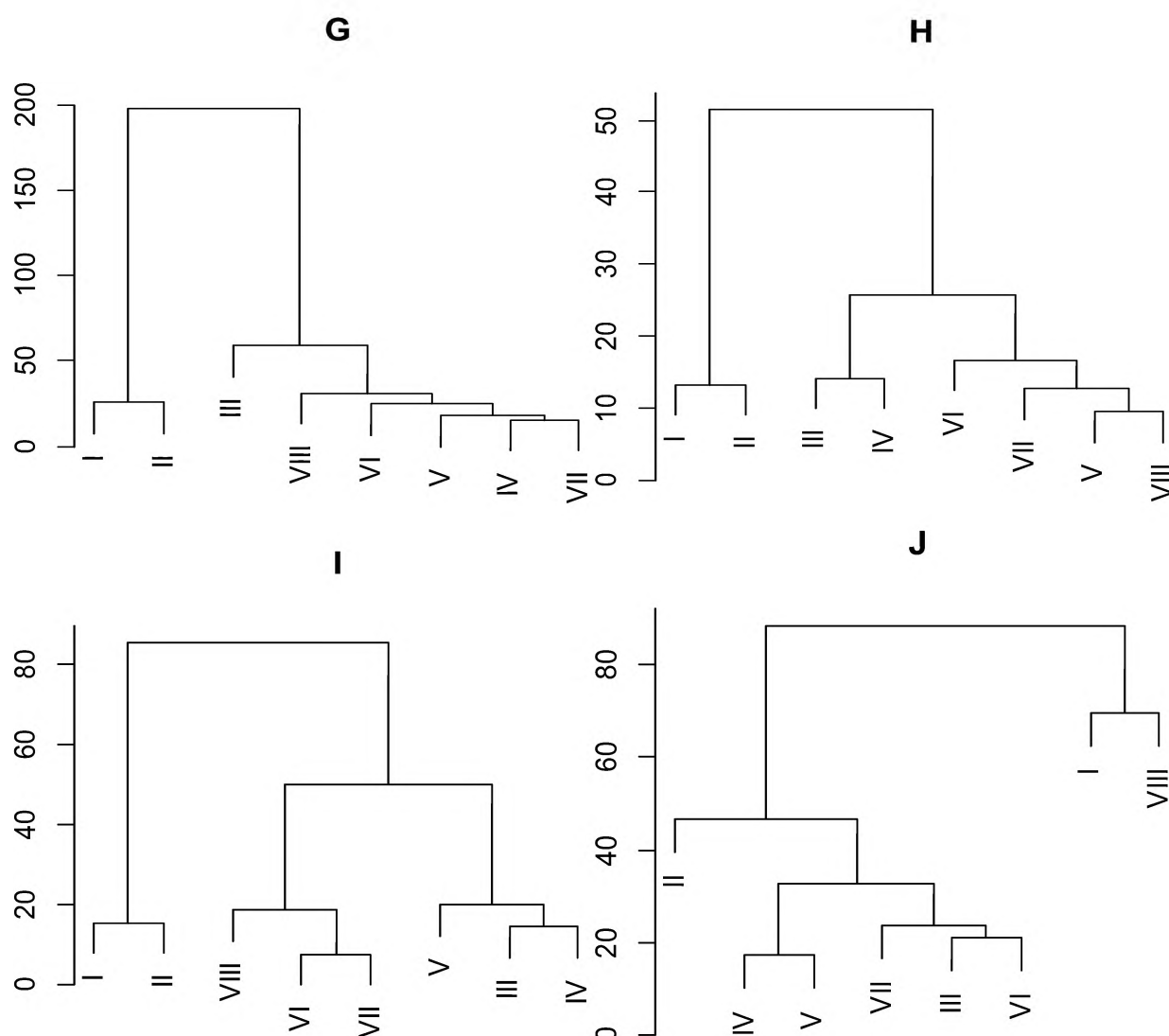
Fig. 65 continued. Cluster analysis (Euclidean distance, Ward method) of successive stages of vegetation based on the total cover of species in study plots 7–10. Explanations: I – 2005…VIII – 2012

These variations were accompanied by significant changes in the values of the species richness of native taxa as well as the biodiversity indices – Shannon-Wiener and Simpson indexes. Non-significant differences in the Shannon evenness index was noted on study plots 2, 3 and 8. The quantitative variation in species richness and diversity does not always seem to be related to the dynamics of the population of small balsam. For instance, on study plot 2-4, 5, 7-8 and 10, the curve of the mean cover of the species over the years of the study is more or less constant and it does not affect the biodiversity of native species irrespective of the value of the cover. On study plot 6, an increase in the biodiversity indices were recorded simultaneously with a decrease in the mean cover of *Impatiens parviflora* (Fig. 71). On the other hand, a decrease in the mean cover of small balsam was accompanied by a decrease in the biodiversity indices although the total cover of native plants increased (Fig. 66).

Fig. 66. Changes in the total mean cover of native plants (Friedman test) against the mean cover of *Impatiens parviflora* (A) species richness of native plants (B) and the biodiversity indices: H – Shannon-Wiener, E – Evenness, D – Simpson index (C) on study plot 1. *** – p<0.001, I – 2005…VIII – 2012

Fig. 67. Changes in the total mean cover of native plants (Friedman test) against the mean cover of *Impatiens parviflora* (A) species richness of native plants (B) and the biodiversity indices: H – Shannon-Wiener, E – Evenness, D – Simpson index (C) on study plot 2. *** – p<0.001, NS – non-significant, I – 2005…VIII – 2012

Fig. 68. Changes in the total mean cover of native plants (Friedman test) against the mean cover of *Impatiens parviflora* (A) species richness of native plants (B) and biodiversity indices: H – Shannon-Wiener, E – Evenness, D – Simpson index (C) on study plot 3. Arrows indicate significant differences between adjacent years. *** – p<0.001, NS – non-significant, I – 2005…VIII –2012

Fig. 69. Changes in the total mean cover of native plants (Friedman test) against the mean cover of *Impatiens parviflora* (A) species richness of native plants (B) and biodiversity indices: H – Shannon-Wiener, E – Evenness, D – Simpson index (C) on study plot 4. Arrows indicate significant differences between adjacent years. ** – p<0.01, *** – p<0.001, I – 2005…VIII – 2012

Fig. 70. Changes in the total mean cover of native plants (Friedman test) against the mean cover of *Impatiens parviflora* (A) species richness of native plants (B) and the biodiversity indices: H – Shannon-Wiener, E – Evenness, D – Simpson index (C) on study plot 5. Arrows indicate significant differences between adjacent years. *** – p<0.001, I – 2005…VIII – 2012

Fig. 71. Changes in the total mean cover of native plants (Friedman test) against the mean cover of *Impatiens parviflora* (A) species richness of native plants (B) and the biodiversity indices: H – Shannon-Wiener, E – Evenness, D – Simpson index (C) on study plot 6. Arrows indicate significant differences between adjacent years. *** – p<0.001, I – 2005…VIII – 2012

Fig. 72. Changes in the total mean cover of native plants (Friedman test) against the mean cover of *Impatiens parviflora* (A) species richness of native plants (B) and biodiversity indices: H – Shannon-Wiener, E-Evenness, D-Simpson index (C) on study plot 7. Arrows indicate significant differences between adjacent years are shown. *** – p<0.001, I – 2005...VIII – 2012
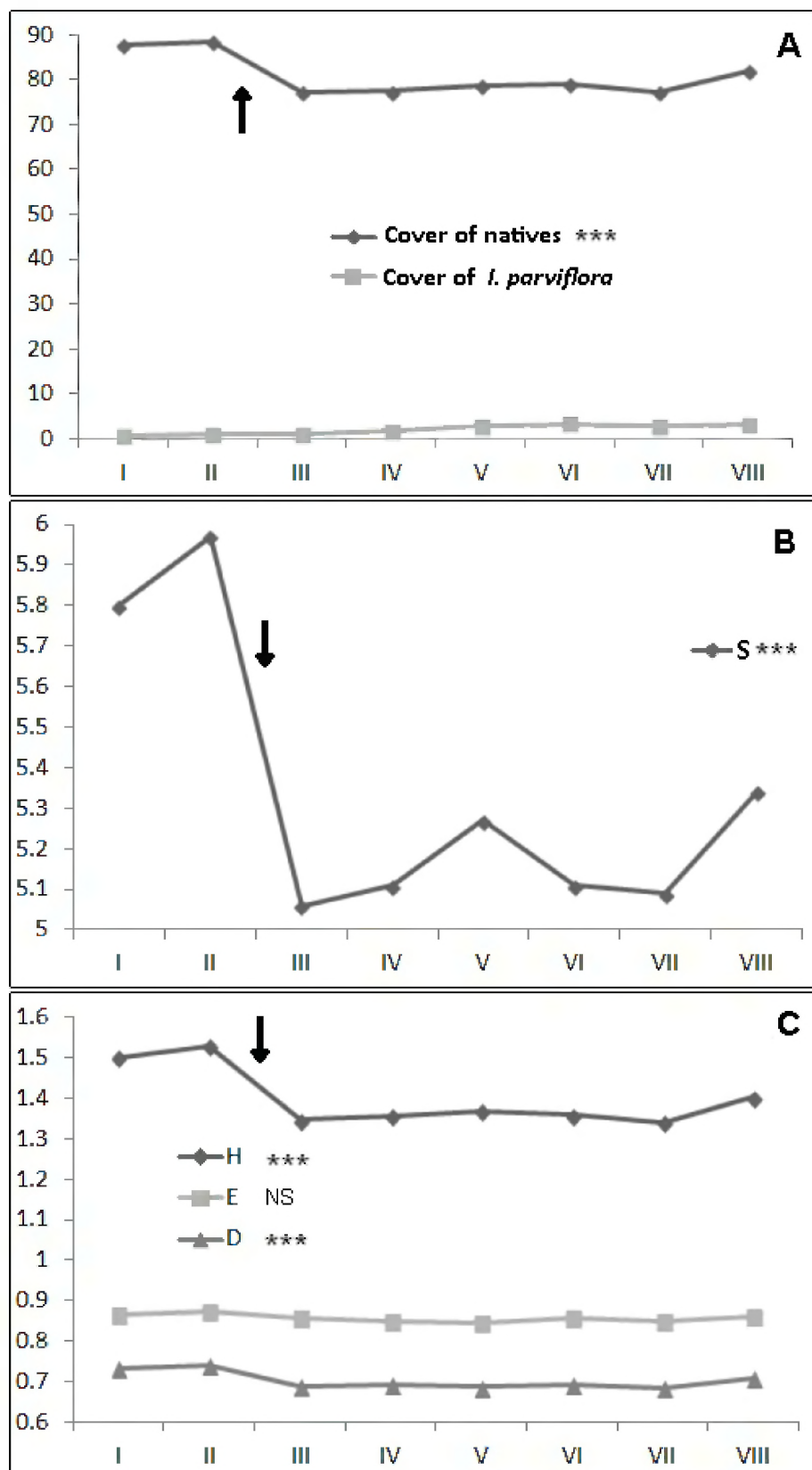
Fig. 73. Changes in the total mean cover of native plants (Friedman test) against the mean cover of *Impatiens parviflora* (A) species richness of native plants (B) and the biodiversity indices: H – Shannon-Wiener, E – Evenness, D – Simpson index (C) on study plot 8. Arrows indicate significant differences between adjacent years. *** – $p<0.001$, NS –nonsignificant, I – 2005…VIII – 2012
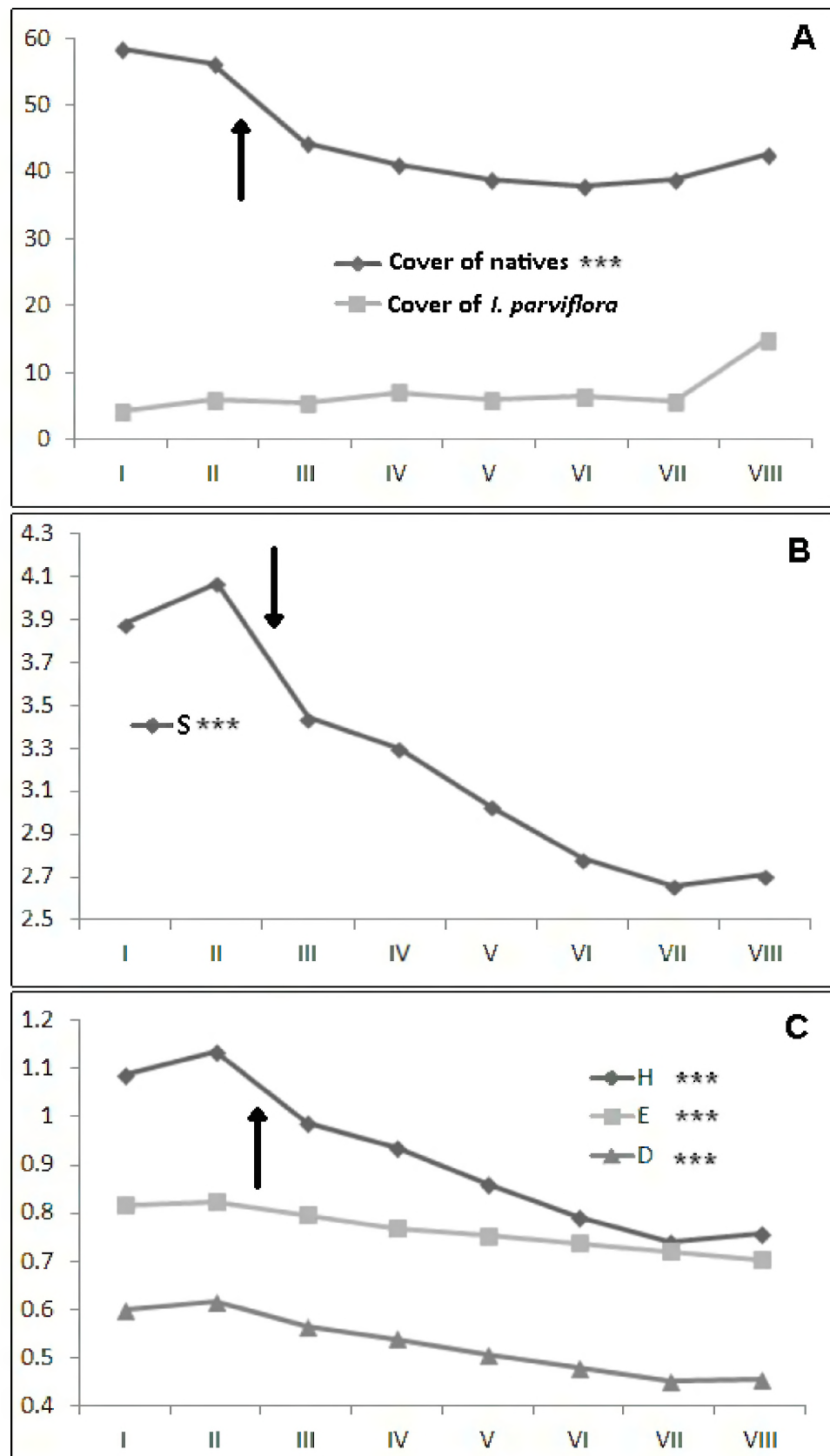
Fig. 74. Changes in the total mean cover of native plants (Friedman test) against the mean cover of *Impatiens parviflora* (A) species richness of native plants (B) and the biodiversity indices: H – Shannon-Wiener, E – Evenness, D – Simpson index (C) on study plot 9. Arrows indicate significant differences between adjacent years. *** – p<0.001, I – 2005…VIII – 2012
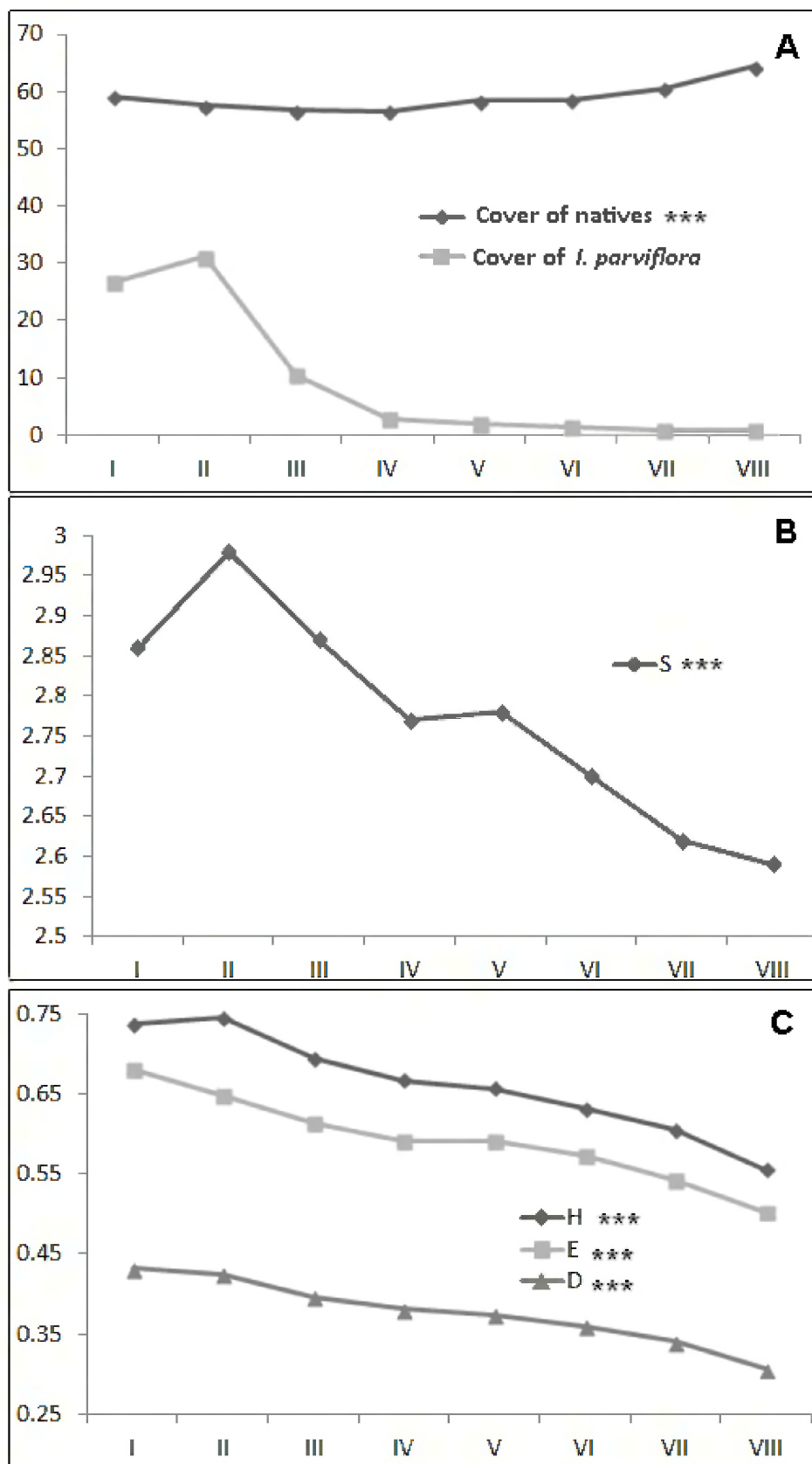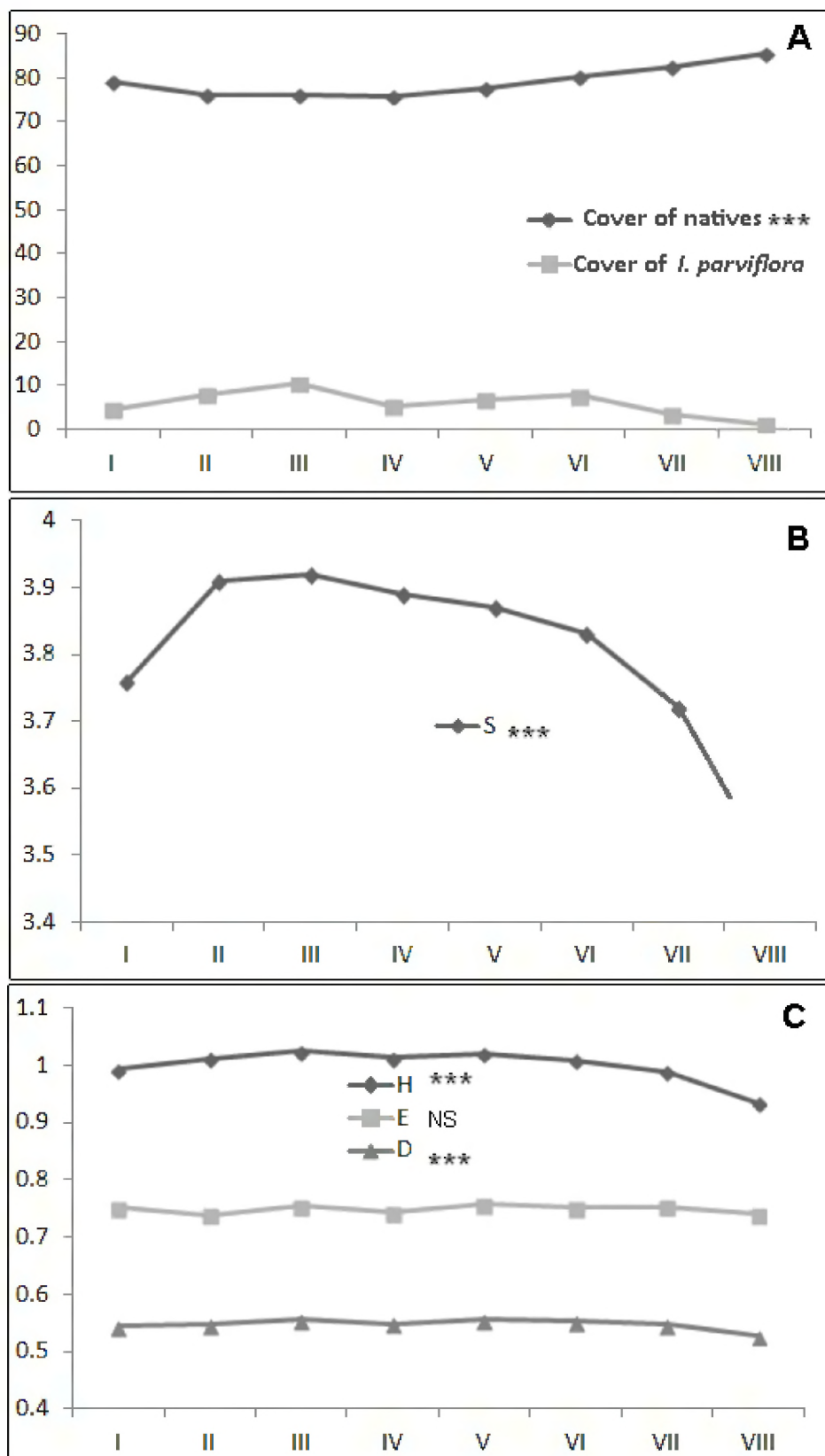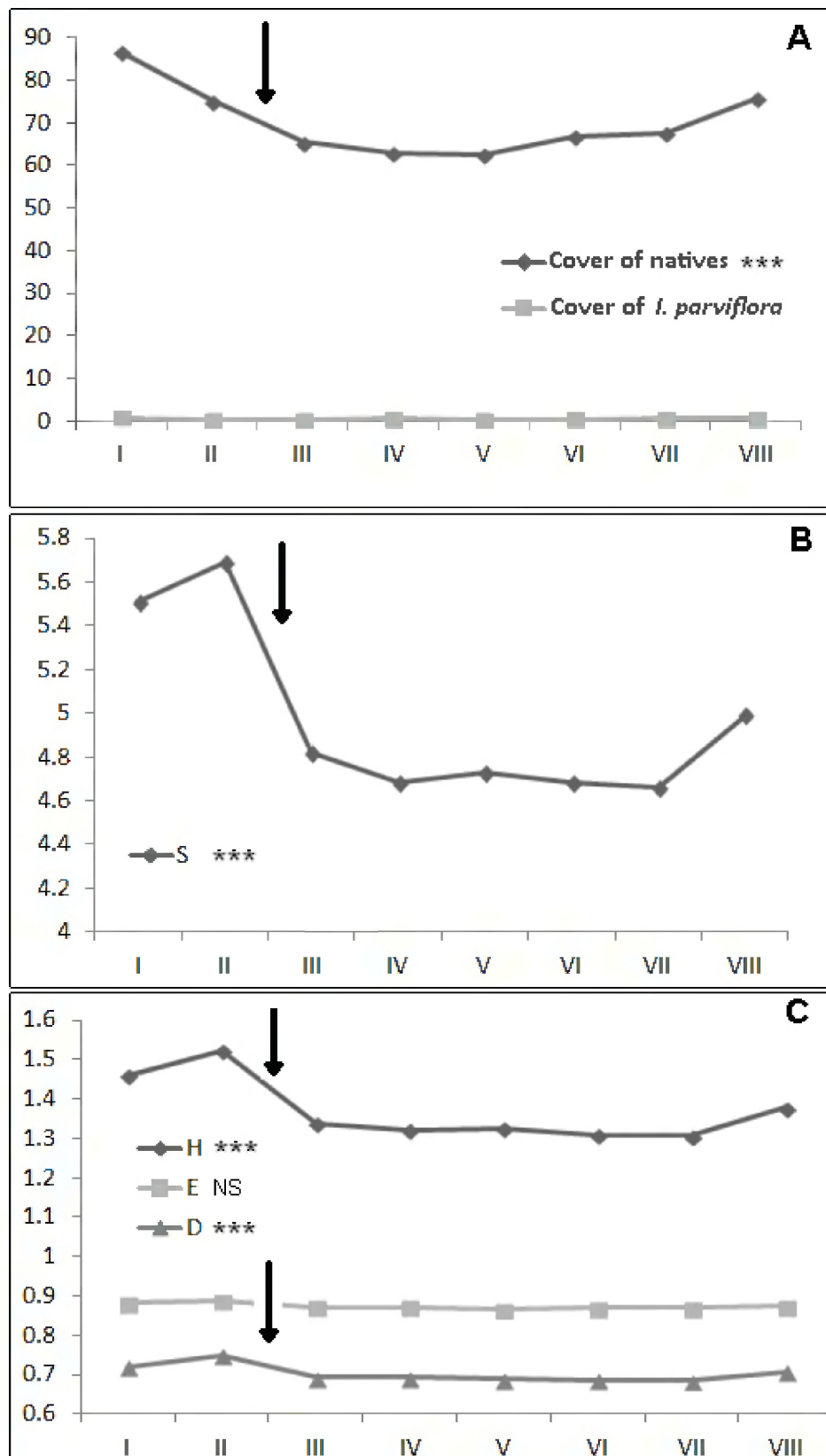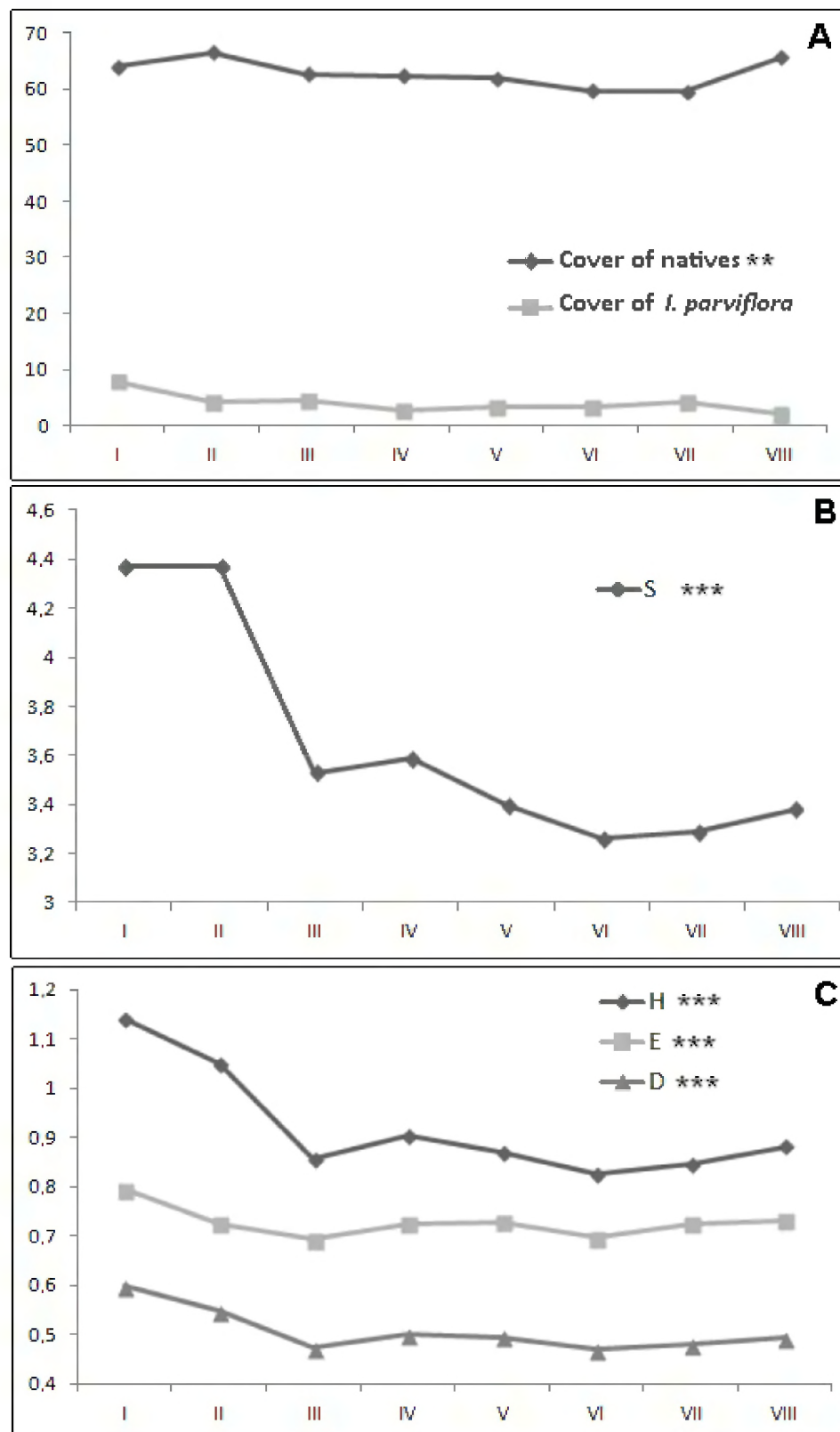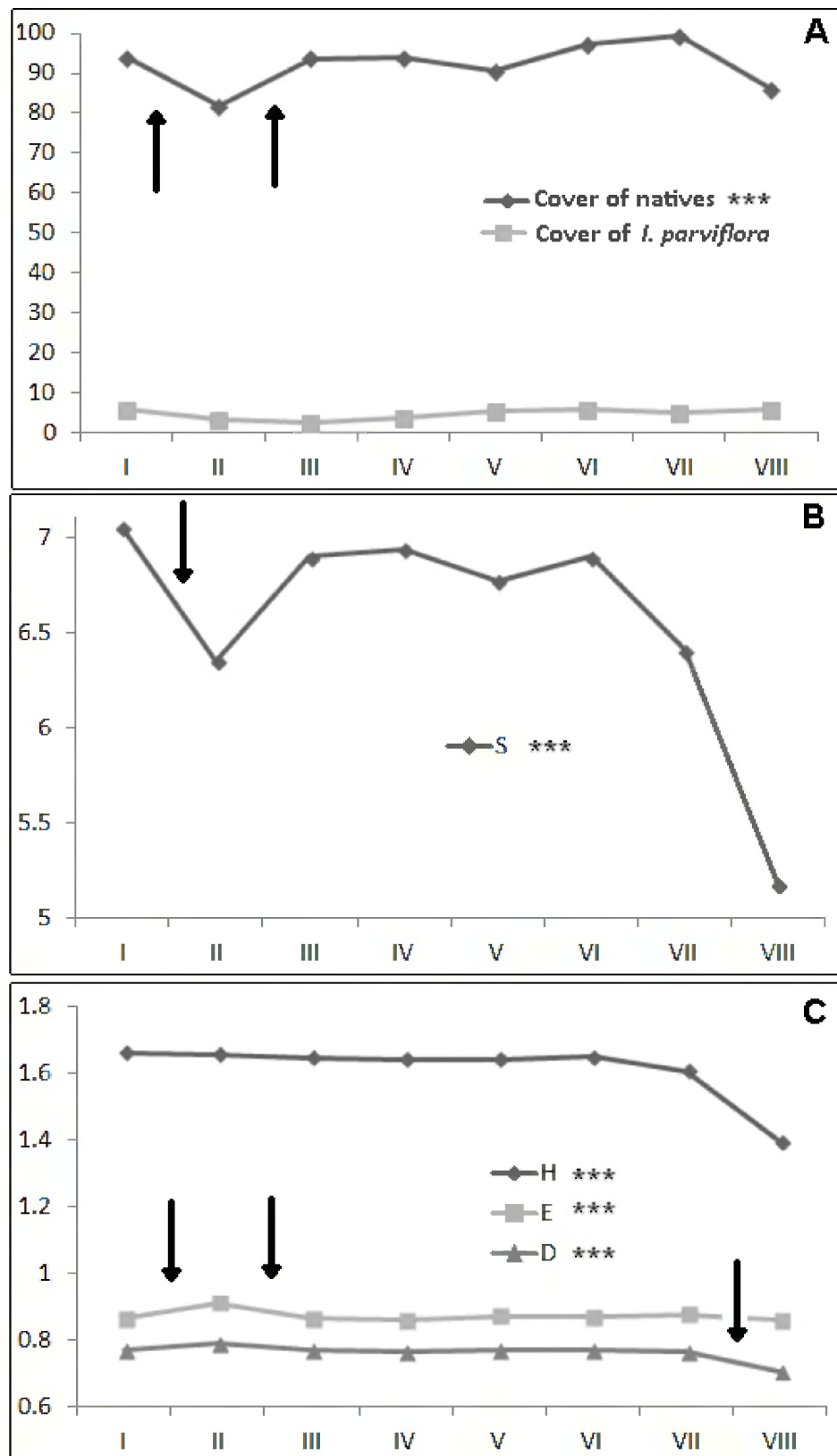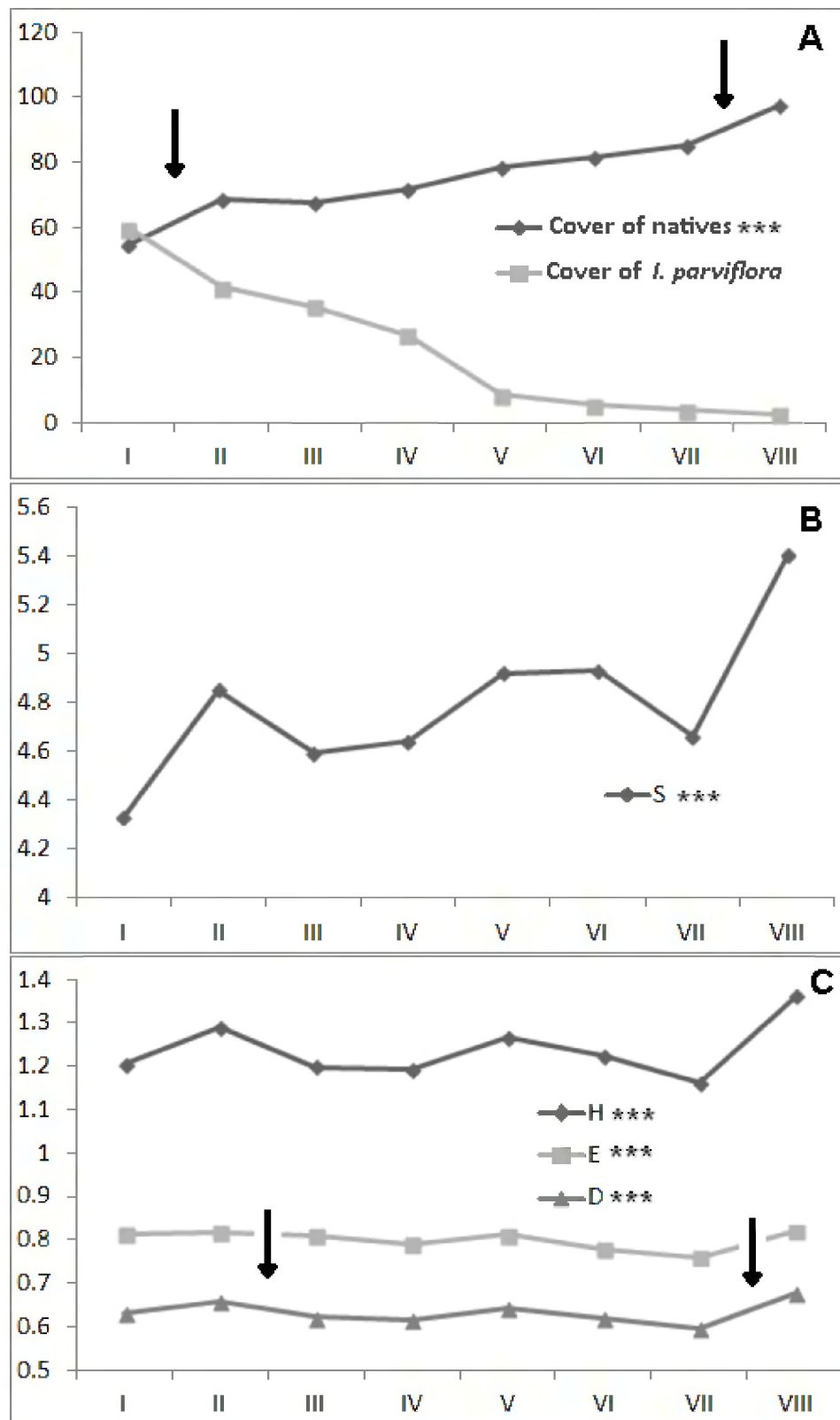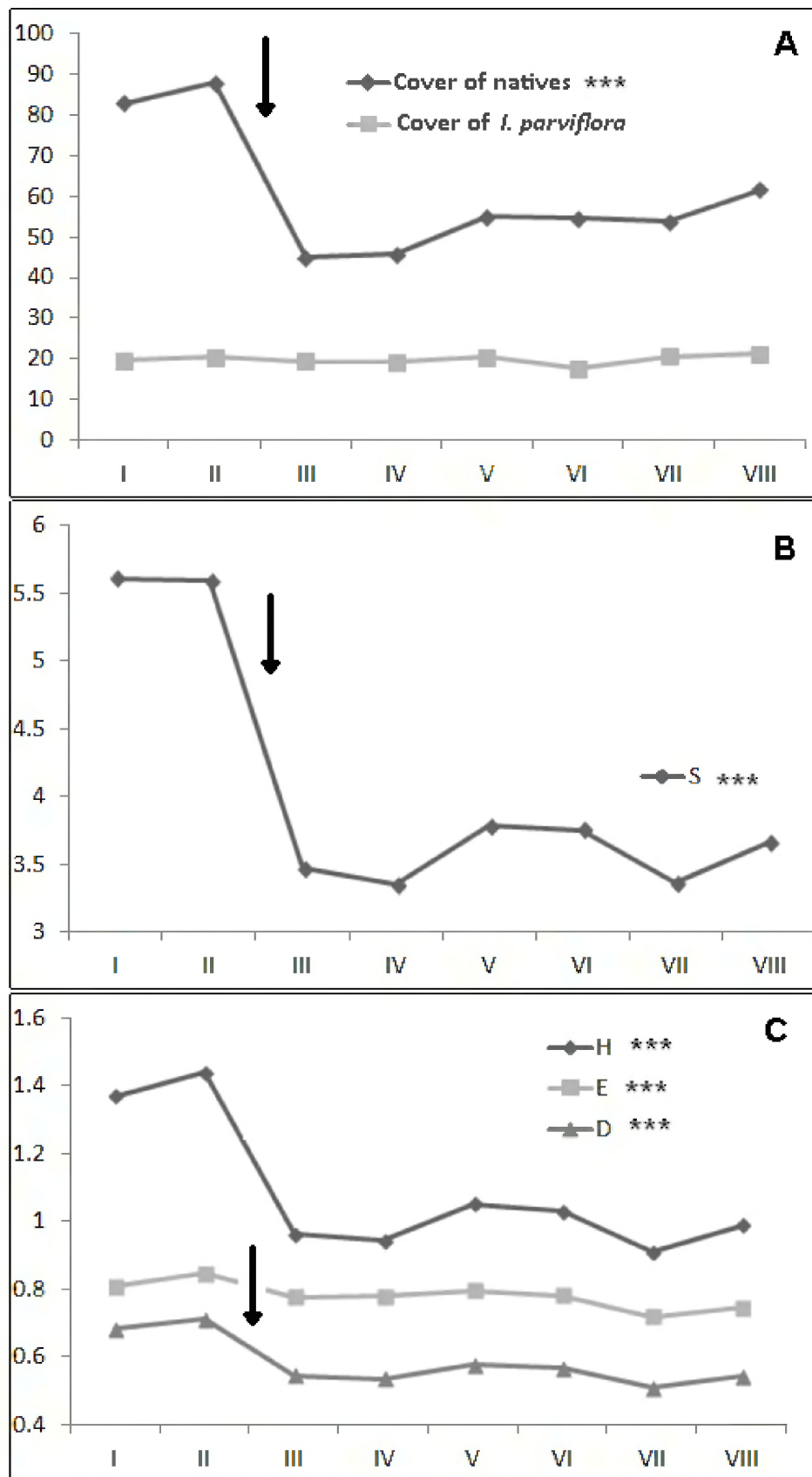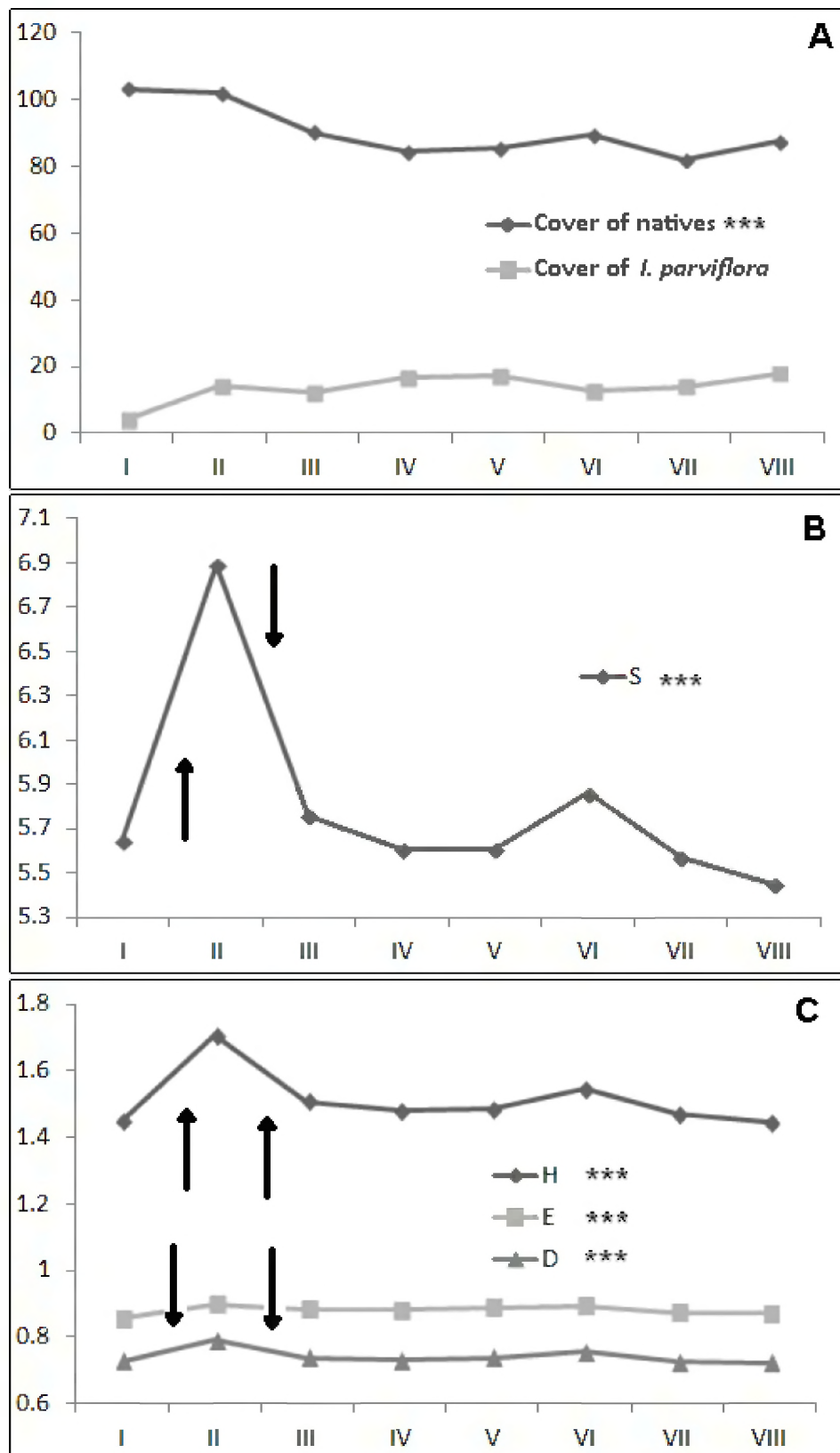
Fig. 75. Changes in the total mean cover of native plants (Friedman test) against the mean cover of *Impatiens parviflora* (A) species richness of native plants (B) and the biodiversity indices: H – Shannon-Wiener, E – Evenness, D – Simpson index (C) on study plot 10. Arrows indicate significant differences between adjacent years. *** – p<0.001, I – 2005…VIII – 2012

The changes in species composition and the cover of native species may have had many different causes. The body of literature on this topic is enormous. There are many examples of long-term studies on permanent plots including forest communities (Faliński 1993 after Falińska 2004; Durak 2009; Dierschke 2006; Łysik 2008, 2009; Kiedrzyński *et al.* 2011; Chmura *et al.* 2013) just to mention few. The high degree of variation concerning species cover over time very often reflects changes that are due to the natural process of succession and regeneration after disturbance, climatic conditions or biocenotic factors. These are mainly air temperature, precipitation or a massive gradation of rodents or insects that are seed predators, respectively. In relatively ecologically stable communities, fluctuations can occur in an herb layer that has been built up by perennial species, for instance geophytes (*Anemone nemorosa*), chamaephytes (*Galeobdolon luteum*) or hemicryptophytes (*Milium effusum*) (Towpasz, Tumidajowicz 1989). Sometimes these phenomena occur within a short period of time, e.g., four years, in populations of *Oxalis acetosella, Anemone nemorosa* and *Galebdolon luteum* (Pirożnikow 1991). Falińska (1991) stated that that succession and the process of the turnover of species is a result of the demographic processes within a population of plants. A similar approach was proposed by Hubbell (2001), who used the term ecological drift to describe the sum of demographic stochasticities for each population in a community. Moreover, he wanted to treat all of the components in a community at the individual level rather than at the species level, which is typical for a neutral versus niche concept of plant communities.

In the present study it was difficult to relate the changes in species composition or species diversity to the dynamics of *I. parviflora*. If there is a casual relationship, then it appears that small balsam is affected species rather than vice versa.

Relations with coexisting species in ground forest flora

A complete list of accompanying species is presented in Appendix 2 based on the number of occurrences on the permanent study plots in the Silesian Upland and the Jurassic Upland. A percentage of frequency was assigned to each species. The most frequent coexisting species are: *Oxalis acetosella, Galebdolon luteum, Galium odoratum, Asarum europaeum, Aegopodium podagraria, Viola reichenbachiana* and tree seedlings of *Fagus sylvatica* and *Acer pseudoplatanus*.

Thirty-three species that are indicators of microsites that have been invaded by small balsam are presented in Table 34. The highest number of indicator species was detected for floodplain forests including *Urtica dioica*, a nitrophilous species on invaded sites, and *Myosotis palustris*, which prefers more humid places than small balsam. *Hedera helix* occupies uninvaded places in

thermophilous beech woods, whereas *Oxalis acetosella* accompanies *I. parviflora*. In some cases, the same species are indicators of either invaded or uninvaded sites depending on type of forest community. One example is *Maiantheum bifolium*, which occupies invaded sites in acidophilous beech and mixed coniferous forests and uninvaded sites in oak-hornbeam forests. In some phytocoenoses of *Tilio-Carpinetum*, the grass *Melica nutans* more frequently occupies invaded sites, whereas in other patches in they occur on uninvaded sites.

Tab. 34. Values of the species indicator IndVal for sites that were invaded or uninvaded by *I. parviflora* in the forest communities that had been distinguished

		invaded		uninvaded		
AU	*Urtica dioica*	0.856	0.001	*Myosotis palustris*	0.835	0.001
	Euonymus europaeus c	0.847	0.001	*Mentha longifolia*	0.707	0.001
	Festuca gigantea	0.707	0.001	*Petasites hybridus*	0.707	0.001
	Lamium maculatum	0.707	0.001	*Stachys sylvatica*	0.7	0.001
	Oxalis acetosella	0.707	0.001	*Rubus idaeus*	0.609	0.001
	Ajuga reptans	0.69	0.001	-		
	Poa palustris	0.63	0.001	-		
CF	*Oxalis acetosella*	0.827	0.001	*Hedera helix*	0.675	0.008
CF	*Fagus sylvatica* c	0.645	0.017	-		
DF	*Hieracium murorum*	0.669	0.022	-		
	Circaea lutetiana	0.622	0.025	-		
LF	*Maianthemum bifolium*	0.662	0.001	-		
TC	*Allaria officinalis*	0.877	0.001	*Maianthemum bifolium*	0.649	0.001
	Melica nutans	0.709	0.001	*Aegopodium podagraria*	0.92	0.001
	Impatiens noli-tangere	0.668	0.001	*Hedera helix*	0.863	0.002
				Melica nutans	0.63	0.003
				Mercurialis perennis	0.816	0.001
				Carex brizoides	0.833	0.001
				Athyrium filix-femina	0.63	0.001
QP	*Geranium robertianum*	0.823	0.001	*Hedera helix*	0.725	0.001
	Galeobdolon luteum	0.664	0.001	*Fagus sylvatica* c	0.627	0.003
	Maianthemum bifolium	0.836	0.001	*Aegopodium podagraria*	0.656	0.002
	Pteridium aquilinum	0.641	0.003	*Convallaria majalis*	0.615	0.001
	Vaccinium myrtillus	0.637	0.002			
RA	*Scirpus sylvaticus*	0.643	0.001	*Chaerophyllum hirsutum*	0.673	0.02

Abbreviations: QP – *Querco roboris-Pinetum*; DF – *Dentario glandulosae-Fagetum*; TC – *Tilio-Carpinetum*; LF – *Luzulo pilosae-Fagetum*; CF – *Carici-Fagetum*, AU – communities of the *Alno-Ulmion* alliance; RA – *Ribeso nigri-Alnetum,* c – in case of trees and shrubs indicate seedlings.

The same situation was revealed for beech *Fagus sylvatica* seedlings. Beech forest sites on which it was present were invaded by small balsam but in mixed coniferous forests it was the other way round.

The relationships between *Impatiens parviflora* and the most frequent species are presented separately for each region (Tab. 35–36).

A negative correlation was found for, among others, *Carex brizoides, Aeogopodium podagraria, Athyrium felix-femina* (Tab. 35) and *Carex sylvatica, Convallaria majalis* (Tab. 36).

It is difficult to state whether a negative correlation indicates a displacement or a shift in biotopic requirements based on the values of the correlation coefficients.

Tab. 35. Values of the Spearman rank correlation coefficient between the percentage of the cover of *Impatiens parviflora* and the cover of native species – a study of the Jurassic Upland

Species	r_S	P	N
Acer platanoides c	0.36	<.0001	130
Acer pseudoplatanus c	-0.14	0.0047	393
Aegopodium podagraria	-0.24	<.0001	515
Ajuga reptans	0.36	0.0029	65
Allaria petiolata	0.75	<.0001	60
Anthriscus silvestris	0.98	<.0001	13
Athyrium filix femina	-0.20	0.0044	202
Carex brizoides	-0.36	<.0001	190
Chaerophyllum aromaticum	0.51	<.0001	74
Dryopteris filix mas	0.29	0.0323	54
Epipactis helleborine	0.42	0.0016	55
Euonymus europaeus c	0.45	0.0006	53
Fagus sylvatica c	0.39	<.0001	450
Ficaria verna	0.49	0.0106	26
Galium odoratum	-0.10	0.043	407
Hieracium murorum	-0.39	0.0121	40
Mercurialis perennis	-0.18	0.0457	124
Oxalis acetosella	-0.09	0.0219	712
Sanicula europaea	0.16	0.05	139
Stachys sylvatica	0.30	0.0081	75
Viola reichenbachiana	0.19	0.0003	341

c – in case of trees and shrubs indicate seedlings

The positive values of the correlation coefficient are mainly related to its coexistence with seedlings or juvenile individuals of trees or shrubs, e.g., *Acer platanoides, Fagus sylvatica* and *Euonymus europaeus*. Among herbaceous species, those that positively correlated are: *Ajuga reptans, Allaria officinalis, Chaerophyllum aromaticum, Dryopteris filix-mas, Stachys sylvatica, Geum urbanum, Luzula pilosa* and many others (Tab. 35–36).

More light can be shed by an analysis of changes in the correlation coefficients of particular study plots among the years of the research (Tab. 37–44). The changes in values of the correlation between *I. parviflora* and *Carex brizoides* can be an example of possible displacement by the latter on study plot 1 (Tab. 37). The values of the correlation decreased with decreasing decrease in the mean cover of small balsam (Fig. 76). Another negative relationship that was observed was the correlation with *Anemone nemorosa*.

Tab. 36. Values of the Spearman rank correlation coefficient between the percentage of the cover of *Impatiens parviflora* and the cover of native species – a study of the Silesian Upland

Species	r_s	P	N
Asarum europaeum	0.56	0.020222	17
Carex sylvatica	-0.53	0.043937	15
Carpinus betulus c	-0.31	0.009054	72
Convallaria majalis	-0.34	0.000410	103
Fragaria vesca	0.28	0.039281	56
Geum urbanum	0.73	0.003008	14
Luzula pilosa	0.22	0.042894	89
Lysimachia vulgaris	0.42	0.012845	34
Oxalis acetosella	0.20	0.000703	292
Rubus hirtus	0.40	0.000358	75
Rubus plicatus	0.60	0.007203	19
Senecio nemorensis	0.72	0.001689	16
Stellaria holostea	0.49	0.015723	24
Vaccinium myrtillus	0.30	0.000001	264

c – in case of trees and shrubs indicate seedlings

Tab. 37. The relations between cover of *I. parviflora* and selected native species in particular seasons: a study of plot 1. In the table Spearman rank correlation coefficient are given

	1	2	3	4	5	6	7	8
Anemone nemorosa	ns	ns	ns	-0.21*	ns	ns	ns	ns
Carex brizoides	-0.66***	-0.52***	-0.33***	ns	ns	ns	ns	ns

Abbreviations: * – p<0.01, ** – p<0.01, *** – p<0.001, ns – non-significant

Fig. 76. Comparison of dynamics tendencies between *I. parviflora* and selected native species exemplified by frequency (lef) and means of cover (right) in particular seasons: a study of plot 1

In study plot 4 in particular vegetation season positive correlation was observed with *Galium odoratum* in first year and two negative ones with *Hieracium murorum* in the next year and in the last year with seedlings of *Acer pseudoplatanus* (Tab. 38, Fig. 77). In total five species negatively correlated with *Impatiens parviflora* in the study plot 5. These are: *Fagus sylvatica, Galeobdolon luteum, Oxalis acetosella, Pulmonaria obscura, Viola reichenbachiana*. Other as cover of *Hedera helix* at the beginning was positively correlated with cover of small balsam but in the last year correlation became negative. With slightly increasing mean cover and frequency the participation of *Fagus sylvatica* seedlings was decreasing. The possible competition with *Viola reichenbachiana* did not result in displacement of any species. The similar situation concern *Galeobdolon luteum* (Tab. 39; Fig. 78).

Tab. 38. The relations between cover of *I. parviflora* and selected native species in particular seasons: a study of plot 4. In the table Spearman rank correlation coefficient are given

	1	2	3	4	5	6	7	8
Acer pseudoplatanus c	ns	Ns	ns	ns	ns	ns	ns	-0.23*
Galium odoratum	0.22*	Ns	ns	ns	ns	ns	ns	ns
Hieracium murorum	ns	-0.25*	ns	ns	ns	ns	ns	ns

Abbreviations: * – p<0.01, ** – p<0.01, *** – p<0.001, ns – non-significant

Fig. 77. Comparison of dynamics tendencies between *I. parviflora* and selected native species exemplified by frequency (lef) and means of cover (right) in particular seasons: a study of plot 4

In study plot 6 there is clear example of decreasing role of small balsam and increasing contribution of *Fagus sylvatica* associated with appearance of seedlings (Tab. 40, Fig. 79). Other species which increased in frequency within the area and in abundance was *Athyrium filix-femina.*

Tab. 39. The relations between cover of *I. parviflora* and selected native species in particular seasons: a study of plot 5. In the table Spearman rank correlation coefficient are given

	1	2	3	4	5	6	7	8
Fagus sylvatica c	-0.20*	-0.23*	ns	ns	ns	-0.33***	ns	
Galeobdolon luteum	-0.27**	ns	ns	ns	ns	ns	-0.26**	-0.03
Hedera helix	ns	0.24*	ns	ns	ns	ns	ns	-0.29**
Oxalis acetosella	ns	ns	ns	ns	ns	ns	-0.20*	ns
Pulmonaria obscura	ns	ns	-0.20*	ns	ns	ns	ns	-0.23*
Ribes nigrum c	ns	0.27**	ns	ns	ns	ns	ns	ns
Viola reichenbachiana	-0.26**	ns	ns	ns	ns	ns	ns	-0.27**

Abbreviations: * – p<0.01, ** – p<0.01, *** – p<0.001, ns – non-significant

Fig. 78. Comparison of dynamics tendencies between *I. parviflora* and selected native species exemplified by frequency (lef) and means of cover (right) in particular seasons: a study of plot 5

The other significant negative correlations with *Hedera helix, Maianthemum bifolium* and *Mycelis muralis* at the beginning of research can be result of quite high frequency in subplots and higher mean cover of small balsam (Tab. 40).

Tab. 40. The relations between cover of *I. parviflora* and selected native species in particular seasons: a study of plot 6. In the table Spearman rank correlation coefficient are given

	1	2	3	4	5	6	7	8
Athyrium filix-femina	ns	ns	ns	ns	ns	ns	-0.28**	-0.26**
Fagus sylvatica c	-0.28**	-0.35***	ns	ns	ns	ns	ns	-0.35***
Hedera helix	ns	-0.20*	ns	ns	ns	ns	ns	ns
Maianthemum bifolium	-0.20*	ns	ns	ns	ns	ns	ns	ns
Mycelis muralis	ns	-0.24*	ns	ns	ns	ns	ns	ns
Vaccinium myrtillus	ns	ns	ns	-0.26**	ns	ns	ns	ns

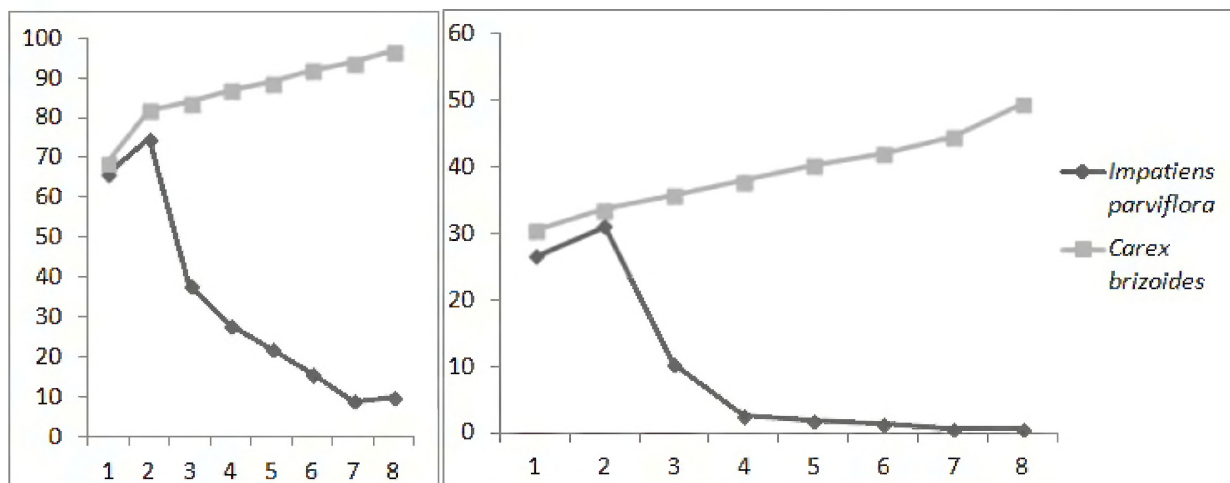Abbreviations: * – p<0.01, ** – p<0.01, *** – p<0.001, ns – non-significant.

Fig. 79. Comparison of dynamics tendencies between *I. parviflora* and selected native species exemplified by frequency (lef) and means of cover (right) in particular seasons: a study of plot 6

In study plot 7 frequency and cover of *I. parviflora* underwent fluctuations but generally it did not change markedly. *Stachys sylvatica* correlated negatively and its frequency a little increased, whereas mean cover decreased (Tab. 41). That could be consequence of exclusion. Native balsam touch me not *Impatiens noli-tangere* decreased in profoundly in frequency and its mean cover. In the last year this species disappeared (Fig. 80).

Tab. 41. The relations between cover of *I. parviflora* and selected native species in particular seasons: a study of plot 7. In the table Spearman rank correlation coefficient are given

	1	2	3	4	5	6	7	8
Carex sylvatica	-0.32***	-0.47***	-	-	-	-	-	-
Fagus sylvatica c	ns	-0.20*	ns	-0.26**	ns	ns	ns	ns
Galeopsis pubescens	ns	0.22*	ns	ns	ns	ns	ns	ns
Geranium robertianum	ns	0.24*	ns	ns	ns	0.23*	ns	ns
Hedera helix	-0.38***	-0.39***	-0.38***	-0.29**	-0.40***	-0.36***	-0.34***	-0.29**
Impatiens noli-tangere	0.26**	0.46***	0.37***	0.27**	ns	ns	ns	-
Sanicula europaea	-0.25*	ns	-0.25*	ns	ns	-0.20*	ns	ns
Stachys sylvatica	0.35***	0.55***	0.39***	0.42***	0.39***	0.42***	0.39***	0.26**
Viola reichenbachiana	0.29**	0.41***	0.32**	ns	ns	ns	ns	0.13

Abbreviations: * – $p<0.01$, ** – $p<0.01$, *** – $p<0.001$, ns – non-significant
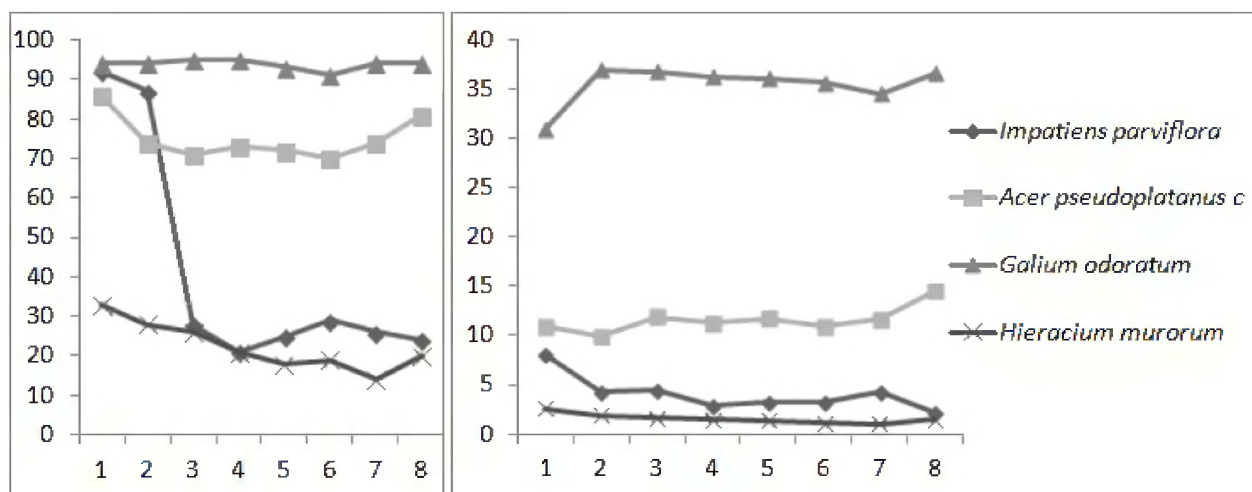

Fig. 80. Comparison of dynamics tendencies between *I. parviflora* and selected native species exemplified by frequency (lef) and means of cover (right) in particular seasons: a study of plot 7

There was significant negative relationship with *Hedera helix* but it seemed that within study plots both species tended to occur in different sites. None of both species was displaced. Other negative correlations are effect of fluctuating dominance of one of the species.

The mean cover of *I. parviflora* weakly increased in study plot 8 what could be reflected by negative correlation with decreasing cover of *Galeobdolon luteum* in the first two and last year

(Tab. 42, Fig. 81). The increasing trend in mean cover of *Oxalis acetosella* was observed what could lead to higher competition or avoidance in microsites occupancy (Tab. 42, Fig. 81).

Tab. 42. The relations between cover of *I. parviflora* and selected native species in particular seasons: a study of plot 8. In the table Spearman rank correlation coefficient are given

	1	2	3	4	5	6	7	8
Acer pseudoplatanus c	ns	ns	0.21*	ns	ns	ns	ns	ns
Aegopodium podagraria	ns	ns	-0.24*	ns	ns	ns	ns	ns
Galeobdolon luteum	0.21*	-0.21*	ns	ns	ns	ns	ns	0.22*
Oxalis acetosella	ns	ns	ns	-0.20*	ns	ns	ns	-0.25*
Sorbus aucuparia c	ns	ns	ns	-0.21*	ns	ns	ns	ns

Abbreviations: * – p<0.01, ** – p<0.01, *** – p<0.001, ns – non-significant

On study plot 9 the increase in the frequency and mean cover by *I. parviflora* led to negative correlations with five coexisting species in the fifth year of the study (Tab. 43, Fig. 82). Despite a very high increase in mean abundance on the subplots, no considerable decreases in other coexisting species were observed.
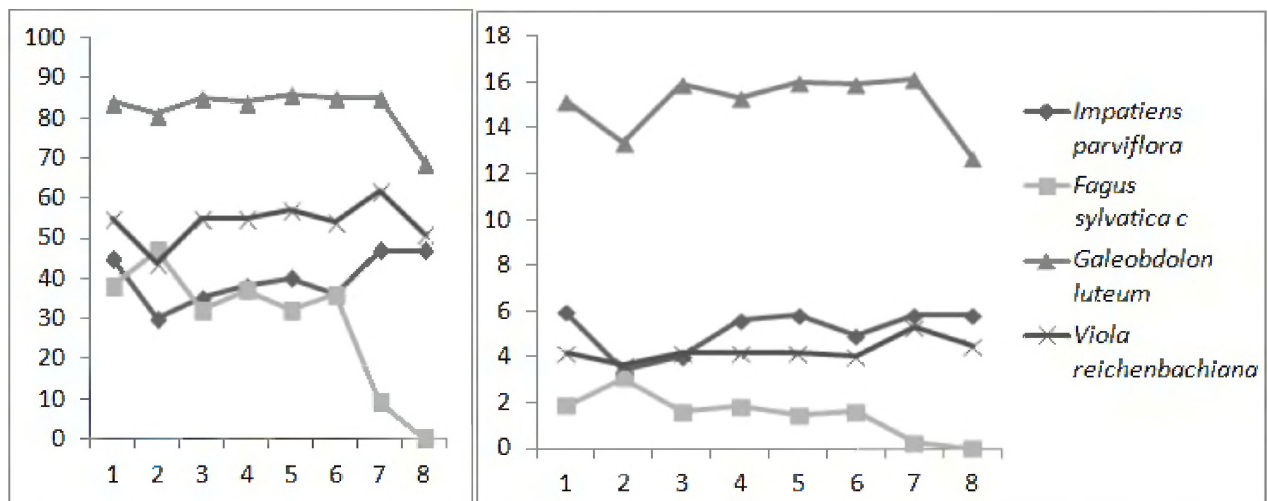

Fig. 81. Comparison of dynamics tendencies between *I. parviflora* and selected native species exemplified by frequency (lef) and means of cover (right) in particular seasons: a study of plot 8

On study plot 10 fifth vegetation season was critical because so many as five species negatively correlated with *I. parviflora* and two species as *Galeobdolon luteum* and *Galium odoratum* were positively correlated (Tab. 44).

Tab. 43 The relations between cover of *I. parviflora* and the selected native species in particular seasons: a study of plot 9. The Spearman rank correlation coefficient is presented in the table

	1	2	3	4	5	6	7	8
Fagus sylvatica c	-0.27*8	ns	ns	ns	-0.22*	ns	ns	ns
Galeobdolon luteum	ns	ns	ns	ns	0.32**	ns	-0.20*	ns
Galium odoratum	ns	0.35***	0.36***	0.24*	0.32**	ns	ns	0.37***
Hedera helix	-0.20*	-0.29**	-0.20*	-0.19	-0.29**	ns	ns	-0.33***
Mycelis muralis	ns	ns	ns	ns	0.27**	ns	ns	ns

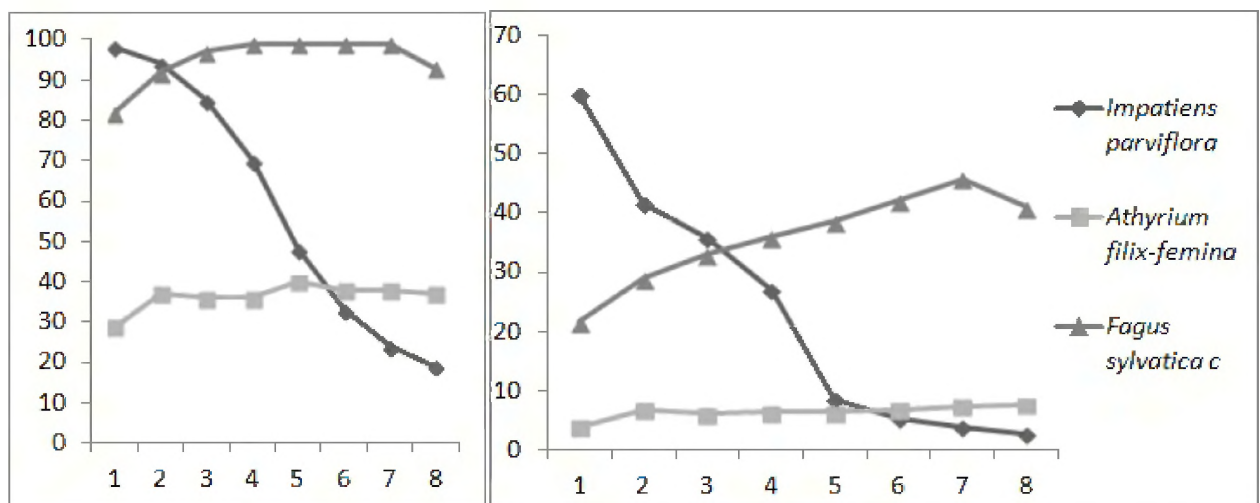Abbreviations: * – p<0.01, ** – p<0.01, *** – p<0.001, ns – non-significant
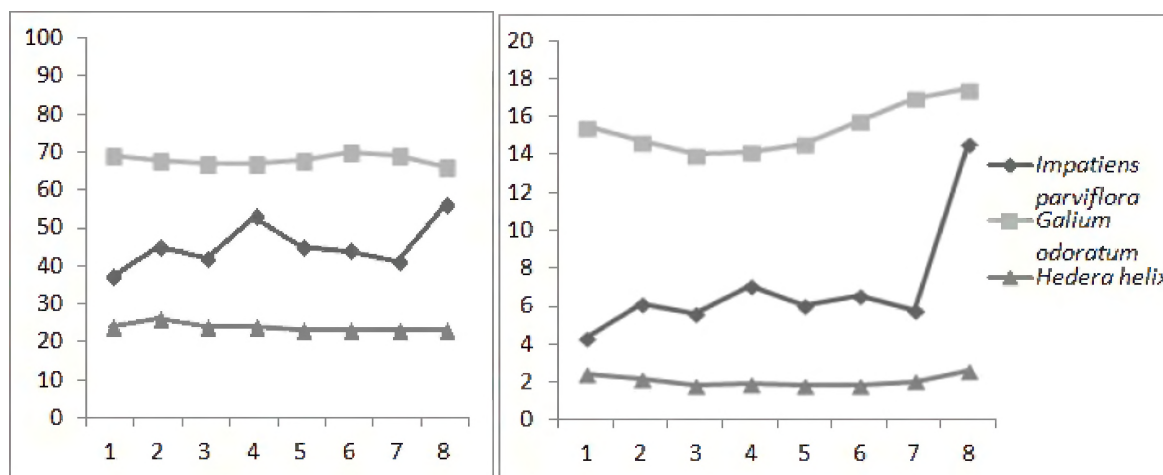
Fig. 82. Comparison of dynamics tendencies between *I. parviflora* and selected native species exemplified by frequency (lef) and means of cover (right) in particular seasons: a study of plot 9.

Only *Asarum europaeum* was plant which weakly decreased in abundance in subplots along increase of cover of small balsam (Fig 83), however, its frequency did not dropped. The increasing role of *Viola reichenbachiana* resulted in appearance of negative correlation with *I. parviflora* but probably both species tended to avoid each other.

Tab. 44. The relations between cover of *I. parviflora* and selected native species in particular seasons: a study of plot 10. In the table Spearman rank correlation coefficient are given

	1	2	3	4	5	6	7	8
Aegopodium podagraria	-	-0.39***	-0.30***	ns	ns	ns	-0.21*	ns
Asarum europaeum	ns	ns	-0.36***	ns	-0.25*	-0.34***	-0.27**	ns
Circaea lutetiana	ns	ns	-0.34***	ns	-0.17*	-0.32**	ns	ns
Galeobdolon luteum	-0.28**	-0.35***	ns	ns	0.14*	ns	-0.47***	ns
Galium odoratum	ns	0.21***	ns	-0.31**	0.22*	0.20*	-0.26**	ns
Maianthemum bifolium	ns	-0.20*	ns	ns	-0.26**	-0.34***	-0.29**	ns
Oxalis acetosella	ns	ns	ns	ns	ns	ns	ns	ns
Sanicula europaea	ns	ns	ns	-0.22*	-0.26**	ns	-0.29**	ns
Viola reichenbachiana	ns	ns	ns	ns	-0.28**	-0.29**	-0.15	-0.24*

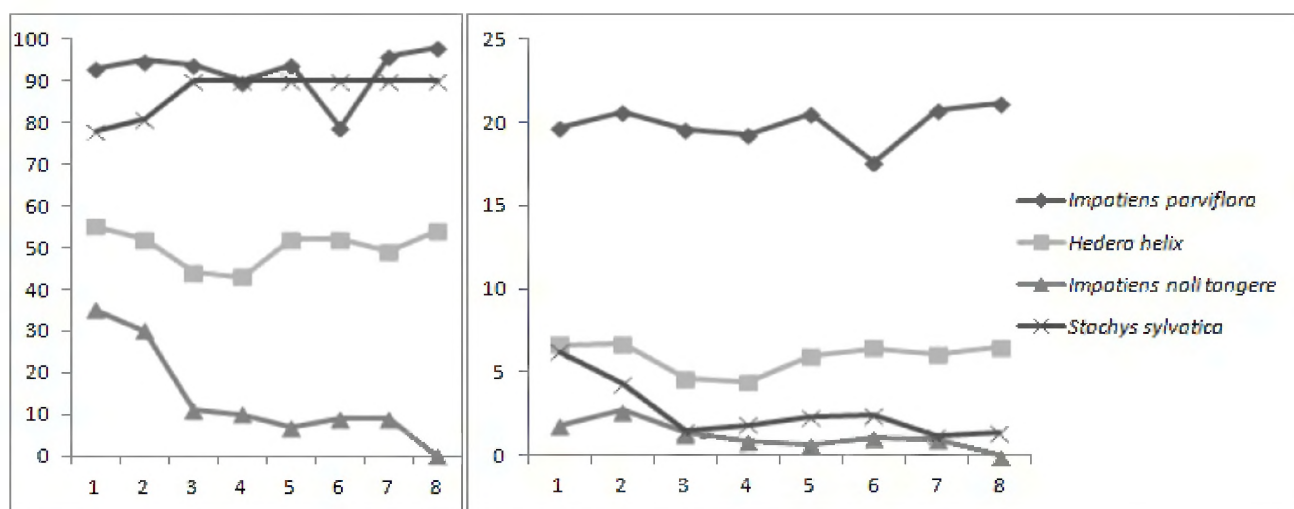Abbreviations: * – p<0.01, ** – p<0.01, *** – p<0.001, ns – non-significant
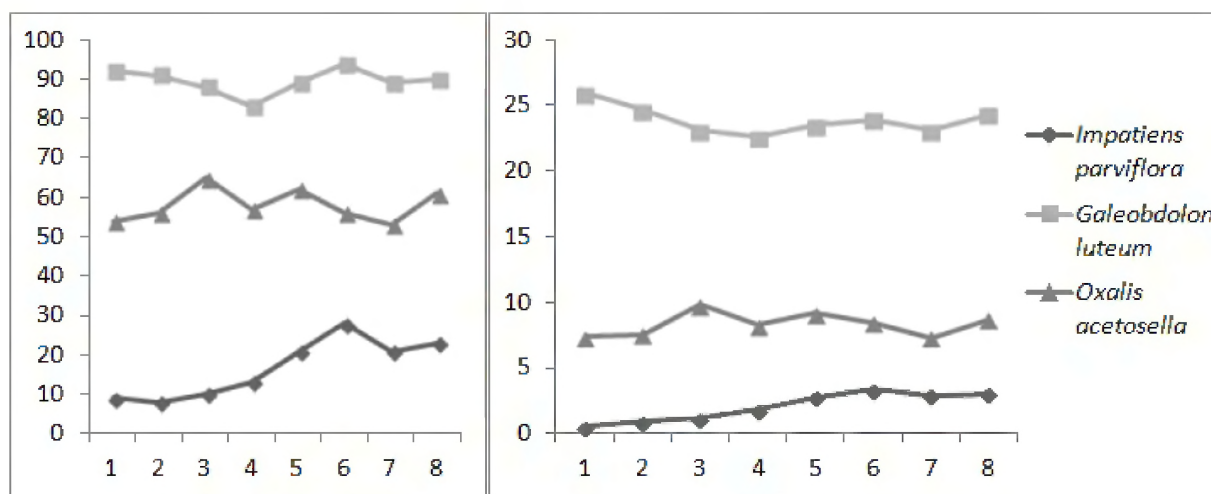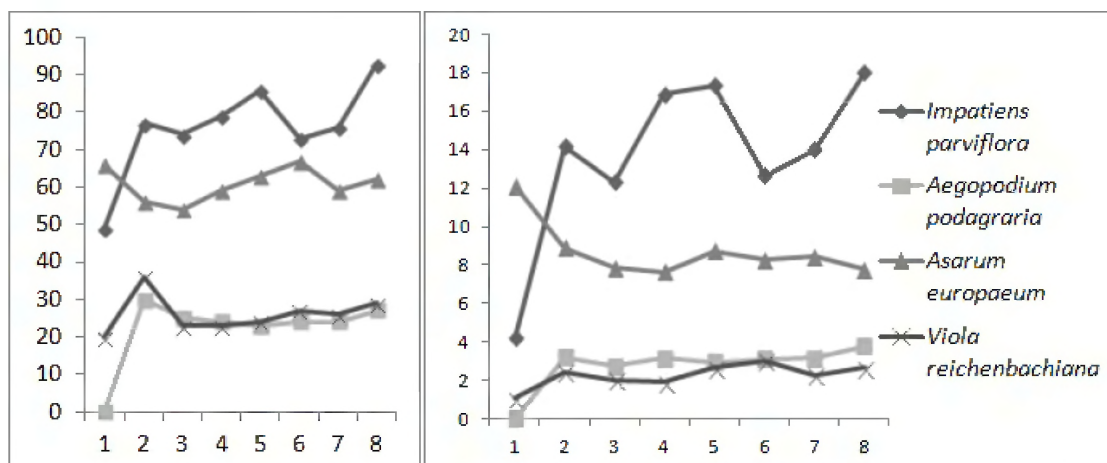
Fig. 83. Comparison of dynamics tendencies between *I. parviflora* and selected native species exemplified by frequency (lef) and means of cover (right) in particular seasons: a study of plot 10

Relations with coexisting species in microhabitats of dead wood complex

The processes of coexistence in the microhabitats that had been distinguished were associated with coarse woody debris as areas near log, logs under canopies, logs under canopy opening, root plates, stumps, treefall disturbances and hollows went in different way. Positive correlation was found for two time series with cover of *I. parviflora* with number of native species occupying the microhabitats that had been distinguished. Only in April negative relationship with total density of native plants was noted (Tab. 45).

Tab. 45. Relationships (Spearman rank correlation) between density of *Impatiens parviflora* and species richness and total density of native species in all in microhabitats associated with coarse woody debris complex combined

Date	Number of native species	Total density of native species
16.04.07	ns	-0.42*
18.05.07	0.63***	0.59***
14.06.07	ns	0.39*
17.07.07	ns	ns
17.08.07	0.68**	0.76***
22.09.07	ns	ns

Both the native cover and density of *I. parviflora* were several fold higher than the total density of native species in all of the microhabitats that were analyzed except for root plates and snags (Fig. 88-89). The highest mean density of *I. parviflora* individuals in areas near logs occurred in July when the native species were the least abundant (Fig. 84). A similar trend was recorded in hollows when the mean density was the highest in June and July (Fig. 85).

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The total density of plants on logs was low and was similar both under canopies and canopy openings (Fig. 86-87) although in conditions with better light availability, the density of small balsam did not decrease quickly and the mean native species survived until the last time series. The highest mean density of small balsam, which exceeded 100 individuals/seedlings, was observed in treefall disturbances although the total density of native plants was not high and was the largest in mid-June (Fig. 90).

Fig. 84. Comparison of the mean number of shoots of *Impatiens parviflora* and the density of native species and the number of native species during a particular time series in areas near logs. Abbreviations: I – 16.04.07, II –18.05.07, III – 14.06.07, IV – 17.07.07, V – 17.08.07, VI – 22.09.2007
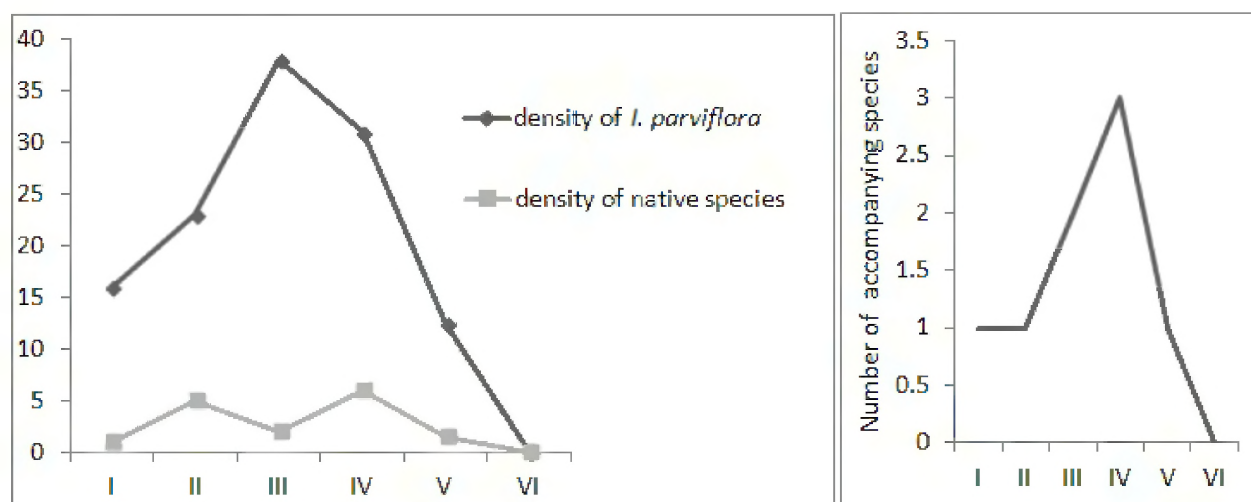
Fig. 85. Comparison of the mean number of shoots of *Impatiens parviflora* and the density of native species and the number of native species during a particular time series in hollows. Abbreviations: I – 16.04.07, II –18.05.07, III – 14.06.07, IV – 17.07.07, V – 17.08.07, VI – 22.09.2007

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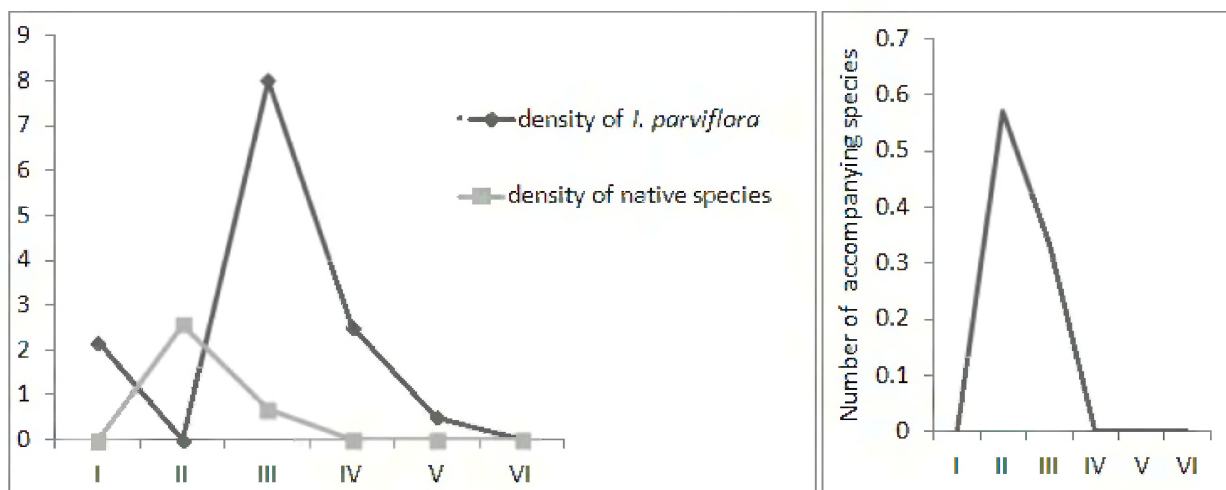
Fig. 86. Comparison of the mean number of shoots of *Impatiens parviflora* and the density of native species and the number of native species during a particular time series on logs under canopies. Abbreviations: I – 16.04.07, II –18.05.07, III – 14.06.07, IV – 17.07.07, V – 17.08.07, VI – 22.09.2007
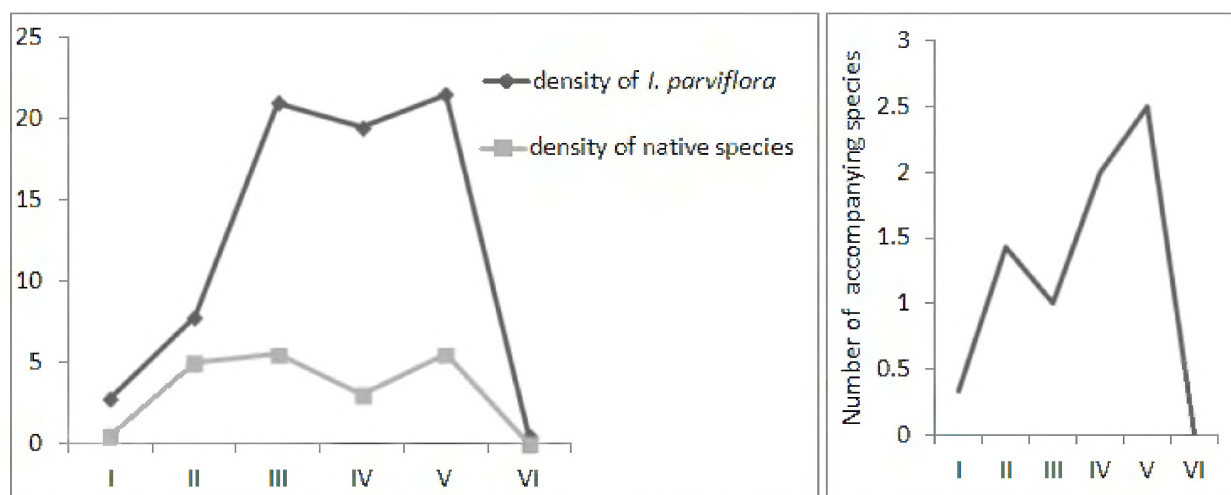
Fig. 87. Comparison of the mean number of shoots of *Impatiens parviflora* and the density of native species and the number of native species during a particular time series on log under canopy openings. Abbreviations: I – 16.04.07, II –18.05.07, III – 14.06.07, IV – 17.07.07, V – 17.08.07, VI – 22.09.2007
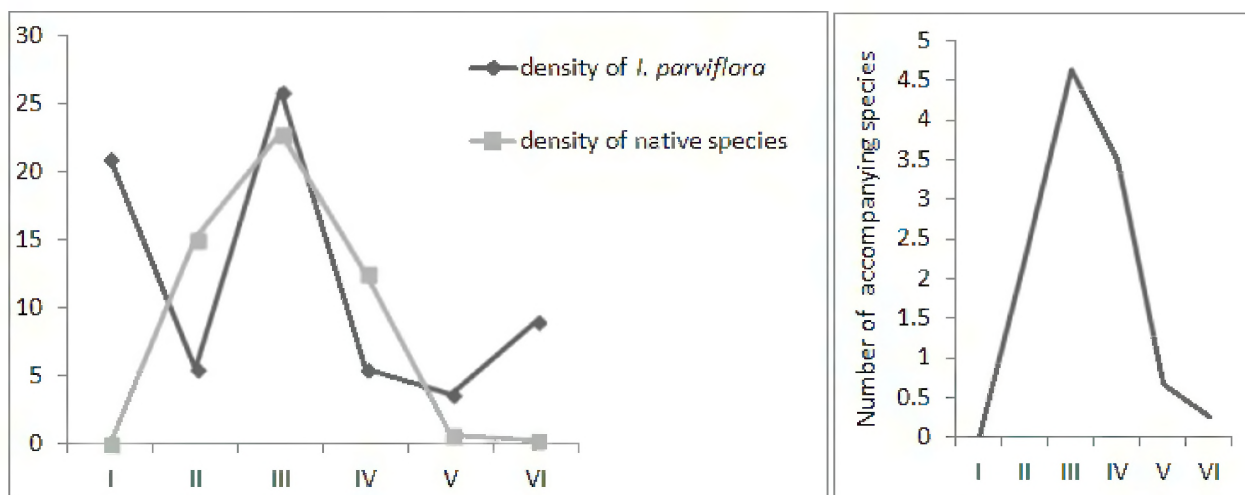
Fig. 88. Comparison of the mean number of shoots of *Impatiens parviflora* and the density of native species and the number of native species during a particular time series on root plates. Abbreviations: I – 16.04.07, II –18.05.07, III – 14.06.07, IV – 17.07.07, V – 17.08.07, VI – 22.09.2007
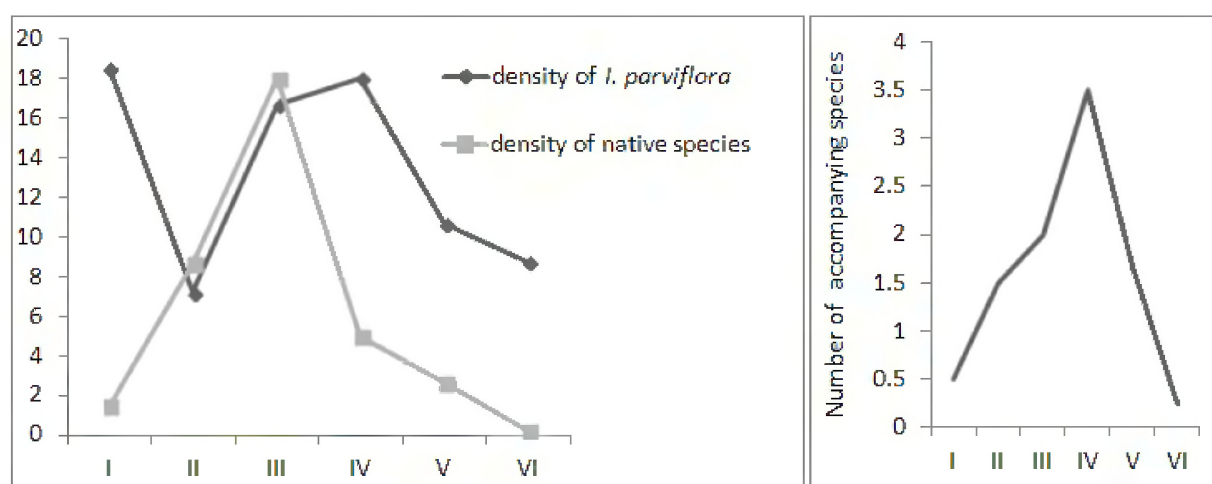
Fig. 89. Comparison of the mean number of shoots of *Impatiens parviflora* and the density of native species and the number of native species during a particular time series on stumps. Abbreviations: I – 16.04.07, II –18.05.07, III – 14.06.07, IV – 17.07.07, V – 17.08.07, VI – 22.09.2007
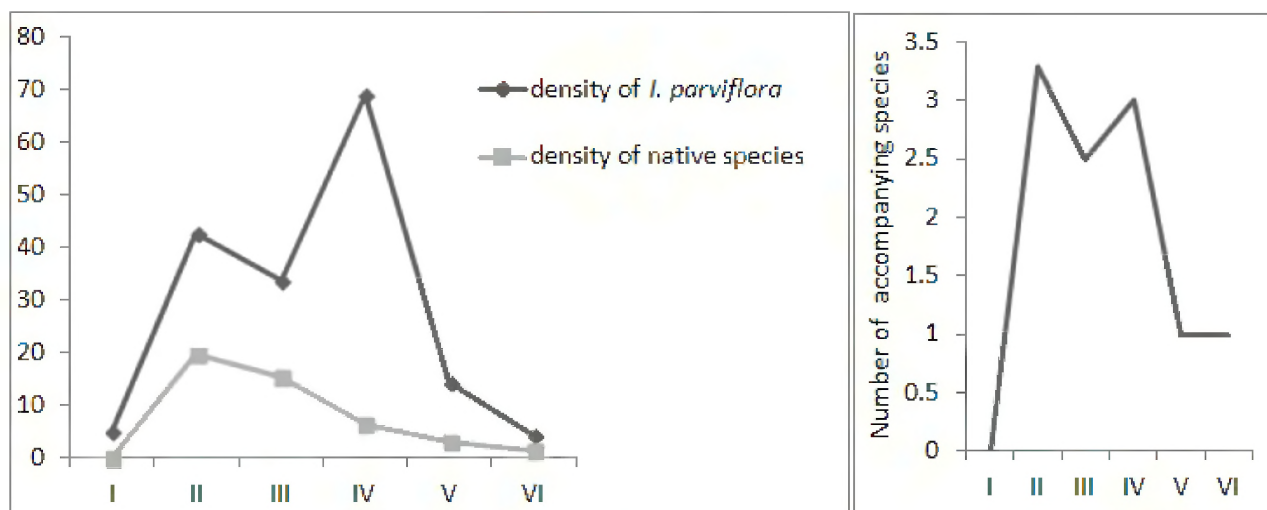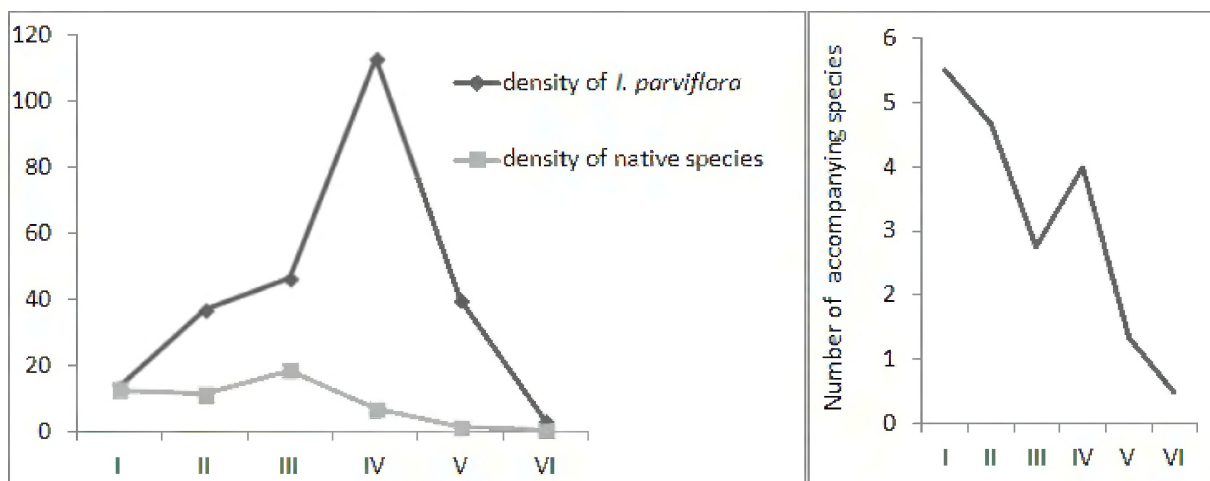
Fig. 90. Comparison of the mean number of shoots of *Impatiens parviflora* and the density of native species and the number of native species during a particular time series on treefall disturbances. Abbreviations: I – 16.04.07, II –18.05.07, III – 14.06.07, IV – 17.07.07, V – 17.08.07, VI – 22.09.2007

One can find various reports about the possible negative impact of *I. parviflora* on other native species or the negative inhibitory effect of native species on small balsam in the literature.

Results by Dobravolskaitė (2012) showed that species such as *Maianthemum bifolium, Hepatica nobilis* and *Galium aparine* do not occur on sites where *Impatiens parviflora* is most abundant. Only strong competitors such as *Urtica dioica* and *Rubus idaeus* occur when the coverage of *I. parviflora* is high. In the oak-hornbeam forest of the Wielkopolski National Park, *Ficaria verna, Carpinus betulus* self seedlings, *Vaccinium myrtillus, Galium odoratum, Pteridium aquilinum* and tuft grasses were found to have a locally strong inhibitory effect on small balsam growth (Piskorz, Klimko 2007). The same species with the exception of *G. odoratum* were observed by Hejda (2012) in the forests of Central Bohemia. Other plants, namely, *Aegopodium podagraria, Athyrium filix-femina, Dryopteris filis-mas, Fragaria moschata, Luzula luzuloides* and *Poa nemoralis* were listed as those that can work as a biocenotic barrier that prevents invasions of small balsam.

According to Łysik (2008), after ten years *Impatiens parviflora* replaced four species: mainly *Galium odoratum*, but also *Asarum europaeum, Mercurialis perennis* and *Galeobdolon luteum*. As she claims the changes that were observed could be a result of natural succession. The species composition had changed from a beech forest to an oak-hornbeam forest. Therefore, it is hard to state that species turnover may be caused by the putative competition ability of small balsam.

Trepl (1984) indicated several species that could be affected by *I. parviflora*. These are: *Impatiens noli-tangere* and perhaps *Ficaria verna, Glechoma hederacea* and *Corydalis cava*. Grass species hinder the growth of the species, e.g., *Dactylis polygama, Arrenatherum elatius* and *Avenella flexuosa*, all of which are present in mixed and coniferous forests. Some species are considered to

be indifferent, e.g., *Urtica dioica, Oxalis acetosella* and *Pteridium aquilinum*. Hegi (1965) also believed that *I. noli-tangere* could be outcompeted, whereas others such as *Moehringia trinervia, Aegopodium podagraria, Geranium robertianum, Galeopsis speciosa* and *Viola riviniana* do not interact with small balsam.

As regards the native congener *I. noli-tangere,* theoretically small balsam shares the same resources and natural enemies and enters into similar plant communities. The results of various studies are ambiguous; for instance Godefroid and Koedam (2010) revealed a significant positive correlation between the cover of small balsam and touch me not balsam, whereas Vervoort *et al.* (2012) reported a significant negative correlation. Łysik (2008) noted an increase in *I. noli-tangere* after ten years in spite of an increase in the abundance of *I. parviflora*. In the present study native balsam had a lower cover that systematically decreased on one study plot and finally the species disappeared although its cover was positively correlated with *I. parviflora*. This indicates that it occupies the same microsites. This was also confirmed by IndVal analysis (Tab. 34). It is not certain that the species was overgrown. Trepl (1984) believes that in moist habitats *I. noli-tangere* keeps the area and dominance whereas can only be overgrown at its suboptimal conditions, i.e. drier habitats. This study and an analysis of the literature confirm this statement.

Previous studies showed that *Carex brizoides* can outcompete *I. parviflora* (Chmura, Orczewska 2004) or that these two species simply avoid each other and differ in the microsites they occupy in oak-hornbeam forests (Chmura, Sierka 2007). Small balsam is overgrown when they are both present, which was shown by the present study where it was observed in the Silesian Upland (Sierka, pers. comm).

It was demonstrated in an analysis of species interactions over time that perennial species, tree seedlings, geophytes, chamaephytes and hemicryptophytes can constitute a barrier against the development of *I. parviflora*. A decrease or displacement of small balsam on microsites depends on fluctuations in the abundance of these plants. A positive cover with other annuals such as *Galeopsis pubescens* or *Geranium robertianum* (annual but sometimes hemicryptophyte) can be explained by the fact that these plants use gaps in the herb layer in the same way as *I. parviflora* does. They have a similar Grime's strategy: – CR and CSR, respectively.

It was previously reported that *I. parviflora* is one of the most common colonizing species on dead beech wood (Chmura 2008c) and hornbeam *Carpinus betulus,* pine *Pinus sylvestris* (Piskorz and Klimko 2001) and oaks (*Quercus* sp) (Nowińska *et al.* 2009). Staniaszek-Kik and Żarnowiec (2012) found the species on 44 elements from among the many various structural elements of dead wood (logs, snags, stumps, treefall disturbances) of *Fagus sylvatica* and *Picea abies* in the Sudeten Mts., mainly on the logs and stumps of *Fagus sylvatica*. It was the most frequent alien species.

No competition was observed among plants that occur on dead logs and other types of similar microhabitats during the vegetation season except for April, during which many of *Impatiens parviflora* seedlings appeared. In some microhabitats such as dead logs and hollows, the number and density of accompanying species was very low, which has an influence on correlation tests. The conditions that occur in microhabitats that are associated with coarse dead wood are not suitable for most plants that are encountered on forest floors due to a lack of moisture and nutrients, thus species that represent a mixed S-R strategy such as *I. parviflora* can thrive in such conditions.

4. Synthesis

4.1. Traits of invasive species

There have been a few attempts to characterize the plant traits that promote invasiveness or weediness. One of the first and most widely cited was the proposal by Baker (1965, 1974), who presented a set of twelve properties of an ideal invader. Later, Baker's list of properties was criticized by Fitter *et al.* (1990) and Perrins *et al.* (1992) for the vagueness of the plant traits that had been defined. Perrins et al. (1993) gave more detailed criteria by which Baker's characters could be scored. These were, among others, 1) no chilling or specific light requirements are required to break dormancy; 2) seed bank type 2 (short-term persistent) and 3 (long-term persistent); 3) relative growth rate of least 1.9 per week, 4) not all meristems are devoted to flowering, 5) neither exclusively inbreeding or outbreeding, 6) use the wind or a wide range of insects for pollination 7), has an average of more than 2,500 seeds per plant and 12) can overgrow other plants. Character 8 or as originally quoted after Baker (1974): "produces some seeds in a wide range of environmental conditions: tolerant and plastic" was impossible to score, whereas 10 and 11 (not presented here), which are related to vegetative growth properties, are only applicable to perennials.

Tab. 46. Set of plant traits considered to be beneficial for species invasiveness (Baker 1965, Rejmánek 2000, Rejmánek *et al.* 2005) vs traits of *Impatiens parviflora*

Biological character of invading plant	Prediction
Individual fitness homoeostasis (=phenotypic plasticity), (="general purpose genotype")	**Yes**
Small seed size	No
High relative growth rate of seedlings and large specific leaf area	**Yes**
Vertebrate dispersal	**Yes**
The size of native geographical range: (the larger, the more invasive the species)	No
Vegetative reproduction	No
No congener(s) in the new invaded area	No
The ability to utilize generalist mutualists	**Yes**
Efficient competition for limited resources (large height, long roots)	No
Characters that favor passive dispersal by humans	**Yes**

Based on these properties Perrins *et al.* (1993) attributed characters 3 and 5 to *I. glandulifera*, which is more invasive in the British Isles. Small balsam, which is a less invasive species, was not evaluated. Further studies summarized the data and reviewed other attempts to distinguish plant traits that are responsible for invasiveness (Rejmánek 2000, Rejmánek *et al.* 2005). The compiled properties are included in Table 46. Only those characters were included that can be estimated in regard to the invasiveness of *I. parviflora*.

Since Baker (1965) it has been widely stressed that phenotypic plasticity (Tab. 45) plays a crucial role in species invasiveness. As regards small balsam, Skálová *et al.* (2013) gave the results of their research on competition among three *Impatiens* spp in a greenhouse experiment. Small balsam showed the highest plasticity followed by *I. capensis* and *I. glandulifera* and *I. noli-tangere*. When phenotypic plasticity was taken into account as an invasiveness predictor for balsams, it turned out that *I. glandulifera* does not fully fit to these criteria as being the most invasive in terms of the competition ability and impact. Indeed, as has been shown *I. parviflora* is a highly diverse species morphologically. In the present study it was demonstrated that its plasticity is nonequivalent in various habitats (Fig. 91). The following methods adapted by Elemans (2004) and Skálová *et al.* (2013) showed that plasticity is the highest in populations that grow along forest paths. The lowest variation was revealed in a floodplain forest in spite of the quite high values of plant size and fecundity, although the individuals that grow there are quite stable in relation to the features studied. The proportional phenotypical plasticity is much higher than the one that was described by Skálová *et al.* (2013). It is the result of other traits that were included into the computations. For instance, number of flowers and fruits were very variable among and within a specific type of habitat. For the purpose of estimating the latter two characters, only generative individuals were measured.

The next feature is a relatively small seed size (Tab. 46). Despite differences in the mean weight of *I. parviflora* between the countries – Poland and Hungary that were described in Chapter 3.2.1., the mean mass of *I. parviflora* was rather high. According to Csontos (2000), who gathered information about the mass seeds for 1,676 species of Hungarian flora, small balsam was classified into the sixth class (4.01-10.0 g per 1,000 seeds) among the eight that had been distinguished. Only 253 (ca. 15%) flora in Hungary belong to the upper two classes. It should be emphasized that the flora pattern for forests is different. Trees and shrub species usually have seeds that are larger and heavier. However, *I. parviflora* does not compete with those species at all. Other species that are annuals and therophytes and that are found in forests, e.g., *Geranium robertianum*, have smaller and lighter seeds (Fitter, Peat 1994).
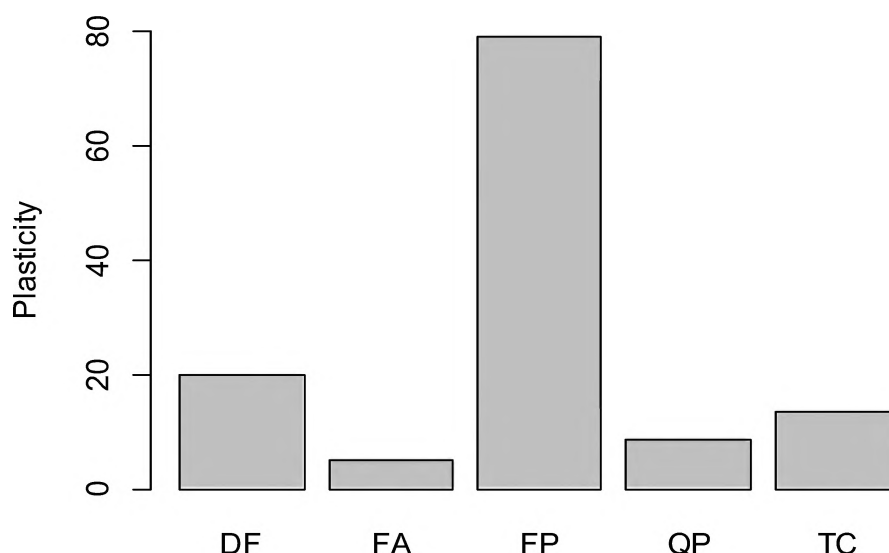
Fig. 91. Plasticity of *Impatiens parviflora* in various types of forest communities expressed as the average ratio between the largest and the smallest value of plant height, length of leaves, width of leaves, number of flowers and number of fruits. Only plants that had flowers and fruits were included. Abbreviations: FA – *Fraxino-Alnetum*, DF – *Dentario glandulosae-Fagetum*, TC – *Tilio-Carpinetum*, QP – *Querco robori-Pinetum*, FP – forest path vegetation

Another important character is the behavior of seedlings (Tab. 46). The present study showed that their ability to occur on different types of substrata is astonishing although their mortality was not high. A comparison with other balsams (Skálová *et al*. 2012) indicated that the traits that are associated with seedlings such as rate of growth and survival make *I. parviflora* a strong competitor at this developmental stage especially when it grows together with *I. noli-tangere*. Small balsam produces a relatively small biomass but at the seedling stage, individuals are larger than its congeners. Despite some reports that crowded populations undergo self-thinning and that the largest growing plants are isolated (Coombe 1956), the intra-specific is lower than the inter-specific competition (Skálová *et al*. 2013).

Vertebral dispersal is still an open question (Tab. 46). To date information about zoochorous dispersal is scarce except for Trepl (1984) and Graae (2002). There are no reports about endozoochory, and it is probable that only epizoochory is possible in this species (Tanner 2008). The quite frequent presence of the species inside hollows or even in the grooves of living trees, which was confirmed in the present study, proves that birds transport seeds. Seeds are most likely transported with dirt on their feet in the same manner as mammals, which was shown by Trepl (1984).

The next three characters do not apply for small balsam at all (Tab. 46). The natural range of the species is relatively small (Meusel *et al*. 1965) , which was stressed by Rejmánek *et al*. (2005) as a noticeable exception. Its invasion success is not predicted by the natural range. The range of

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adventives is much greater nowadays. As an annual and monocarpic plant, it reproduces only by seeds. Its native congener *I. noli-tangere* is present in Europe; moreover, both species frequently coexist.

Although small balsam is believed to have a positive impact on native fauna because it is a host for *Impatienticum asiaticum* and a rich fauna of aphidophagous insects (Schmitz 1998), its attractiveness for pollinators is low. It does use pollinators, mainly *Syrphidae* and perhaps also *Hymenoptera*, but this requires further research. The research by Perez (2006) and Vervoort *et al.* (2011) showed that *Impatiens parviflora* exhibits autonomous self-pollination reaching an 81.4% fruit set that is linked to complete self-compatibility and no inbreeding depression was found for this plant, which gives the species a great advantage to spread independent of the availability of pollinators. The situation is similar with arbuscular mycorrhiza, which is not obligatory only facultative, but when it is present it is beneficial for species (Chmura and Gucwa-Przepióra 2012).
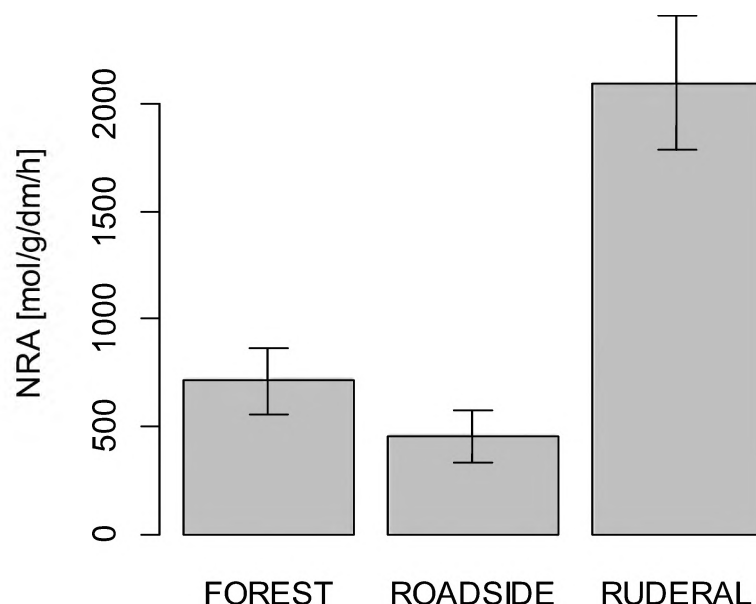
Fig. 92. Activity of nitrate reductase (NRA) in *Impatiens parviflora* leaves in various types of habitats (Chmura *et al*, in prep)

Small balsam is not an efficient competitor species (Tab. 46). As an annual species, which is on average rather short lived and which has a shallow root system, it does not possess the mechanisms that are necessary to compete with other species through shading or root competition. The only possible weapon it possesses is allelopathy. Some of the studies that have reported on allelopathy (Vrchotová *et al.* 2009; Csiszar, Bartha 2008; Csiszar *et al.* 2012) focused on laboratory experiments. It is not known how to relate these finding to natural conditions.

Finally, the role of humans is not to be underestimated. Firstly, humans are the main vector of seed transport (transport with vehicles, timber) and it facilitates long-distance dispersal. Secondly, due

to human activity artificial habitats – semi-natural and ruderal are more frequently colonized by small balsam than natural ones.

Rejmánek (2000) when describing the biological attributes of invasive alien species mentioned nitrogen fixation, which along with other ecophysiological traits can be useful in explaining species invasiveness but we still do not have sufficient data. As far as nitrogen fixation in *I. parviflora* is concerned, the first preliminary results indicate that the metabolism of nitrogen compounds in this species varies among different habitats. The activity of nitrate reductase (NRA) that was measured directly in the field was higher in ruderal habitats in which the nitrogen input from the decomposition of biomass and wastes is higher than in other habitats (Fig. 92). Diekman and Falkengren-Grerup (2002) believe that NRA has a lower value of prediction of plant responses to atmospheric deposition and enhanced soil nitrogen levels; however, the prediction of the nitrogen content in soil is dependent on the choice and accuracy of the methods that are applied (Krywult, Bielec 2012). An analysis of NRA would probably be useful in predicting the degree of the rate of nitrogen fixation among different habitats and among different species and in testing the theory of fluctuating resources *sensu* Davis *et al.* (2000).

4.2. Causes of biological invasions

Among the various theories that seek to explain the invasions of plants, some seem to be useful in the prediction of the success of *I. parviflora*. Others, which are based on previous research, have failed. One of the first attempts chronologically was Darwin's Naturalization Hypothesis (Tab. 47). This corresponds with predicting the character "no congener(s) in the new area" (Tab. 46). It not at all applicable in the case of invasions of *Impatiens parviflora* as well as the entire genus *Impatiens*. According to this theory, exotic genera with native representatives should be less successful because of an overlap in the use of resources and because they share the same natural enemies. In Europe in addition to small balsam other balsams, other species such as *I. glandulifera, I. balfourii* and *I. capensis* are both naturalized and invasive (Adamowski 2008; Schmitz, Dericks 2010; Perrins *et al.* 1993). Moreover, some studies have suggested that native congeneric *I. noli-tangere* can be displaced by exotics including small balsam (Daumann 1967; Faliński 1998b).

There can be little doubt about the methods that were applied in these studies. Some insights are given in the work by Skálova, Pyšek (2009), who in a germination experiment showed that *I. noli-tangere* can be outcompeted by *I. parviflora* and *I. glandulifera*, which is the best congeneric competitor.

Tab. 47. Major hypotheses explaining plant invasion (based on Hiero *et al.* 2005; Richardson *et al.* 2011) vs. hypotheses explaining invasion success of *Impatiens parviflora* in introduced range

Hypothesis name	Definition	Authors of hypothesis	Prediction	References
Darwin's Naturalization Hypothesis (DNH)	Alien species with close native relatives in their introduced range may have reduced chances of establishment and invasion	De Candolle (1855), Darwin (1859)	No	Dostál *et al.* (2012), Dostál, Palečková (2011)
Enemy Release Hypothesis (ERH)	Exotics are released from natural enemies that control their population growth	Darwin (1859), Williams (1954), Elton (1958), Keane, Crawley 2002 Colautti *et al.* 2004	No	Najberek *et al.* (2011), Dostál (2010)
Evolution of Invasiveness	Exotics experience rapid genetic changes linked to new selection pressures in the novel environment	Blossey and Nötzold (1995), Lee (2002), Stockwell *et al.* (2003)	No	Komosińska *et al.* (2006), Kupcinskiene *et al.* (2013)
Empty Niche Hypothesis	Exotics utilize resources unused by the locals	Elton (1958), MacArthur (1970)	Yes	Trepl (1984), Piskorz, Klimko (2001), Chmura (2008)
Fluctuating Resources Theory Of Invasibility	Fluctuations in resource availability enhances community invasibility	Davis *et al.* (2000)	Yes	Eliáš (1999)
Novel Weapons Hypothesiss	Exotics bring novel ways of biochemical interaction to recipient communities	Callaway and Aschehoug (2000), Bais *et al.* 2003	Yes(?)	Vrchotová *et al.* 2009; Csiszar, Bartha 2008; Csiszar *et al.* 2012
Disturbance Hypothesis	Exotics are adapted to disturbances' type and intensity that are novel to natives	Gray (1879), Baker (1974)	Yes	Obidziński, Symonides (2000), Chmura, Sierka (2006)
Biotic Resistance Hypothesis	Species-rich communities are more resistant to invasion than species-poor communities	Elton (1958), MacArthur (1970, 1972)	Yes	Obidziński, Symonides (2000), Chmura, Sierka (2006), Hejda (2012)
Propagule Pressure Hypothesis	Variations in levels of invasion among recipient communities are due to differences in the number of exotics arriving in the community	di Castri (1989), Williamson (1996), Lonsdale (1999)	Yes	Coombe (1956), Trepl (1984)
Evolution Of Increased Competitive Ability Hypothesis (EICA)	Exotics obtained increased competitive ability through the relaxation of herbivore pressure	Blossey and Nötzold (1995)	Maybe	Schmitz (1998)
Competitive Release Hypothesis	Alien species may be released from competition in habitats with novel competitors or no competitors	Sorte *et al.* 2010	Maybe	-

In a pot experiment the growth and final biomass of *I. parviflora* was not affected by the presence of native balsam (Dostál, Palečková 2011), but it was rather the other way round, in the absence of an invasive competitor, *I. noli-tangere* displayed traits that were divergent with regard to the size of plants, phenology and morphological plasticity (Dostál *et al.* 2012). These studies proved or no effect of native representative of genus on behavior of *I. parviflora* or even its competition capability.

Another theory that seems to be able to interpret the success of non-native plants is the Enemy Release Hypothesis (Keane, Crawley 2002). It assumes that adventive species leave most of their natural enemies (fungal pathogens, phytophagous insects, seed predators, etc.) at home. To date there has been no study that compared the species composition of potential enemies in native and invasive ranges. However, the predictability of the theory was tested in different ways as was shown by Dostál (2010 and literature cited therein). He studied the survival rate of native and alien species including *I. noli-tangere* and *I. parviflora* in relation to the effect of fungal pathogens, seed predators and treatments with fungicide and seed predator exposure or both treatments in the comparison with a control. His research partially supported the theory for other species taken into analyses. Seed predator enclosures significantly increased the proportion of seeds that were retrieved in both balsams, whereas the application of fungicide caused a decrease in *I. parviflora*. A similar effect of seed predators on a native congener was revealed. In general, a larger number of seeds of small balsam were retrieved in the control than was observed in the control of *I. noli-tangere*, which might indicate that the seeds of *I. parviflora* were attacked less by enemies in comparison with native balsam. However, the author did not present statistical analyses for this result. Moreover, he emphasized that the enemies were limited to two groups – rodents and insects and fungal pathogens and the lack of some significance in some analyses meant that these results should be treated with caution. As regards the fungi samples, they were taken from mixed forests for both balsam species. The type of habitat and soil has an impact on species composition of fungi. Falencka and Grzywacz (1984) observed that pathogenous fungi predominate on seeds of *I. noli-tangere* in oak-hornbeam forests whereas there are saprophytic fungi in floodplain forests. Najberek *et al.* (2011, in prep) conducted a series of tests comparing the number of individuals, invertebrate species and the amount of damage by fauna in pairs and triples of species. For a pair of *I. parviflora* and *I. noli-tangere* only in 8% ERH was supported. Other analyses included a comparison between two regions – lowland, mountain or the type of population – wildlife, cultivation etc.

Two theories are similar, namely the Empty Niche Hypothesis (Elton (1958) and the Fluctuating Resources Theory of Invasibility (Davis *et al.* 2002) both of which assume that non-

native species can penetrate an unoccupied niche or can utilize unused resources. The latter additionally takes into account temporal changes in the availability of resources. A disturbance that leads to the short- or long-term release of resources into the environment can be beneficial for exotic species. For instance, thinning tree stands during forest management practices or a windthrow of trees both contribute to more suitable light conditions on the forest floor. For photophilous and also for shading-tolerant plants like small balsam such a disturbance promotes its development. As some studies have demonstrated empty niches for *I. parviflora* are those that are associated with coarse dead wood – dead logs, treefall disturbance sites, etc. Small balsam is a very frequent species in such microsites. Those findings are also in accordance with the disturbance hypothesis.

Disturbed habitats such as forest paths are corridors for the migration of species and can be transitional habitats for the future invasion of a species into inner forest. Such a relationship between small balsam and forest path environments, which was exemplified by a 4,300 ha forest complex, was found by Godefroid and Koedam (2004b). In a much larger area, i.e. the Silesian Upland (ca 4,000 km^2), which is situated in Southern Poland, an inventory of 52 forest complexes (Chmura 2004) showed that *I. parviflora* mostly occurred along forest roads and paths, followed by its presence in forest interiors and along the forest edges that are associated with fire lines and forest borders and ruderal sites (clear-cuts, dumping sites) (Fig. 93). The median cover along forest borders was the highest but was only significantly higher than populations under a tree canopy. The presence/absence of *I. parviflora* in a forest interior was under impact of abundance of the species in non-forest habitats (Logistic regression, $\chi^2 = 6.2042$; p=0.0127).

The theory that assumes an evolution of invasiveness (Tab. 46) in terms of rapid genetic changes also does not predict invasiveness of small balsam. When alien invasive species colonize a new area, genetic variation is often lower than in the source population for two reasons – the founder effect and self-compatibility (Novak, Welfley 1997; Amsellem *et al.* 2000). Even Coombe (1956) claimed that the genetic variation in small balsam is rather low. The reason that was given is the lower morphological variation in Europe than in its native region. Recent genetic studies in Poland and Lithuania, respectively, (Komosińska *et al.* 2006; Kupcinskiene *et al.* 2013b) showed that there are no significant differences in genetic variation among distinct populations and also showed that small balsam was introduced many times, thus the founder effect did not occur and did not lead to a genetic drift toward the newly adapted European population genetically.
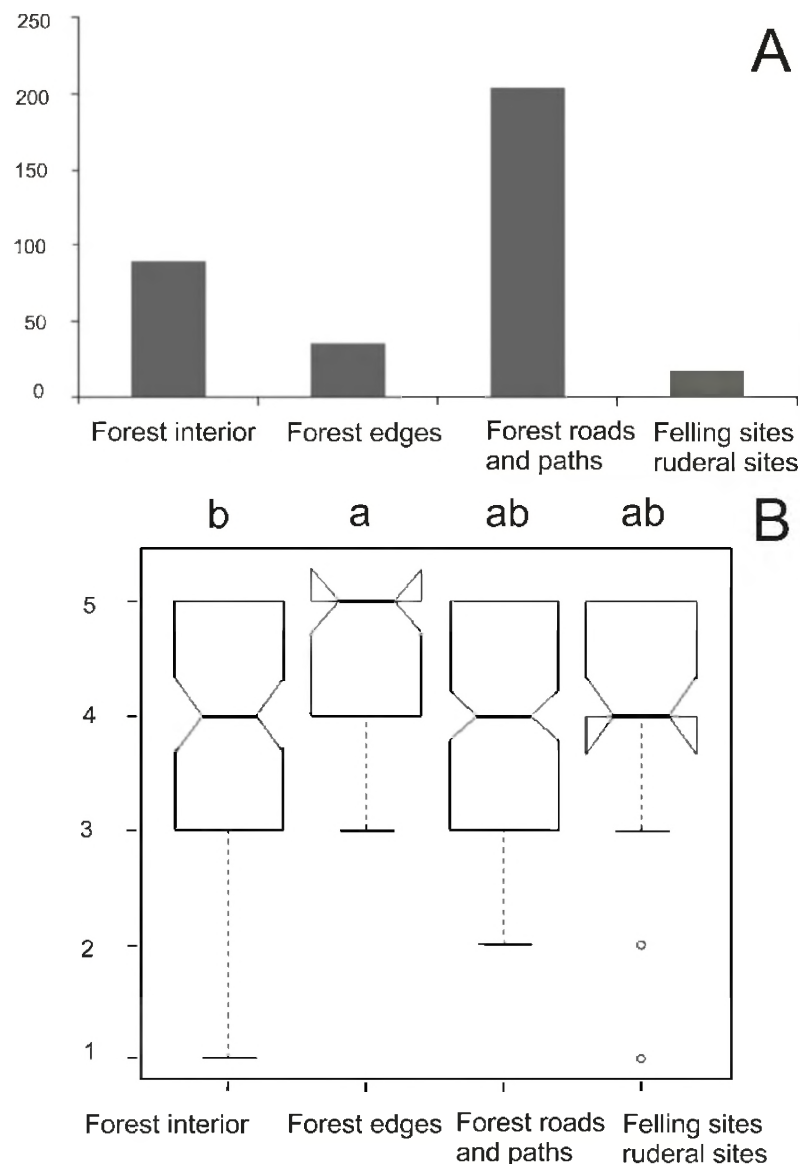
Fig. 93. Frequency (A) and (B) differences in mean cover-abundance of *Impatiens parviflora* in the four main groups of habitats within the forest areas of the Silesian Upland based on Chmura (2004) but recalculated (Kruskal-Wallis test, χ^2 = 8.2855, df = 3, p<0.05, Conover test as post-hoc procedure)

This is somewhat congruent with Galera and Sudnik-Wójcikowska (2010) who pointed out many escape events from botanical gardens at the beginning of invasions of *I. parviflora*.

The Novel Weapons Hypothesiss (Tab. 47) has been a relevant theory since the allelopathic attributes of the species were recognized. Field tests are needed to estimate the effect of chemical substances on the condition of coexisting species. The evolution of increased competitive ability hypothesis (EICA) (Tab. 47) is unclear in relation to small balsam. On one hand, almost no herbivores (except for roe deer) were recorded feeding on plants. On the other hand, a comparison of the morphological variations between the adventive and native region did not indicate a higher robustness of the species in invasive ranges, which could be attributed to a shift in biomass

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allocation due to its release from the pressure of herbivores. Still there is a lack of data that present morphometric studies of small balsam in its native East Asian and invasive ranges in Europe. The scarce information in literature about biology and ecology of *I. parviflora* within its native range is responsible for the lack of acceptance or rejection of the Competitive Release Hypothesis (Tab. 47). For all that is known about habitats occupied by small balsam in its native range, it can be inferred that the species grows in the same or equivalent biotopes as *I. noli-tangere* in Europe. Future comparative ecological studies in two ranges, native and adventive, will help to answer to many questions. The need for conducting such studies was pointed out by Hierro *et al.* (2005).

4.3. Model of *Impatiens parviflora* invasion

Some efforts have been made to summarize the biological traits as well as the intrinsic environmental and anthropogenic factors that enhance the success of an invasion of *I. parviflora*. According to the general model of invasion proposed by Faliński (1968, 1998ab), like many alien species *I. parviflora* underwent several phases of naturalization, which was called "neophytism", i.e. to become a neophyte species. The first phase is "epehemerophyte/ergasiophygophyte" = "casual weed" – the occurrence in anthropogenic and semi-natural habitats such as parks, gardens. The next phase is the stage of euneophyte in which the species occurs in natural habitats, i.e. forests and forest margins. The last stage is a post-neophyte phase when a new xenospontaneous community is formed instead of the natural community. In this phase more alien species are capable of penetrating into the habitat and becoming a permanent element of the vegetation. This is the equivalent of the invasion meltdown concept. During the process of neophytism, neophytes have interactions with other resident species. Small balsam exhibits a suppletive action and in a further phase a substitutive action by which it displaces *I. noli-tangere* (Faliński 1998b, Kujawa-Pawlaczyk 1991). This model is rather general and descriptive. Few biological attributes of small balsam are taken into account.

Eliáš (1999) introduced the abilities and limits of an invasion of *I. parviflora* into Europe. Moreover, he listed the environmental factors (human-induced changes and the effects that are related to them) that support an invasion of the species. The following characters were included for abilities: 1) extreme plasticity in shade tolerance; 2) high efficiency of energy conversion; 3) high reproductive capacity, even in deep shade; 4) lower nutrient demands; 5) very few parasites or predators in Europe. In turn, the limits include: 1) droughts in summer; 2) low temperatures in early spring; 3) high temperatures in spring and summer; 4) long-distance dispersal by humans and animals.

Only human-induced changes were mentioned as environmental factors. These are: 1) the thinning of the tree canopy, which creates canopy openings, increasing the irradiance near forest floor, partial understory disturbance and seed dispersal; 2) the removal of the tree canopy, which leads to clear-cut areas and forest margins, changes in the microclimate, large disturbances of the undergrowth, substrate disturbances and seed dispersal and 3) trampling by humans and animals, which results in partial disturbance of the undergrowth and seed dispersal.

The majority of the plant traits and factors that were mentioned are relevant. However, there is a lack of information about mutualistic interactions and how natural environmental (disturbance) factors might enhance the spread and invasion by this species. Some items such as a high efficiency of energy conversion or a high reproductive capacity should be specified. These traits varied considerably among the invaded habitats.

Tanner (2008) distinguished "risk and impact factors". The main attributes of species invasiveness were: fast growth, gregariousness, propagules that can remain viable for more than one year, a high degree of mobility locally, being the pioneer in disturbed areas, proven invasive outside its native range and tolerance of shade.

While the majority of these traits are valuable, there are exceptions. Small balsam does not create viable seeds that last for more than one year. Single seeds were sometimes viable for more than one season but there were too few to consider this variable as important for invasiveness. Indeed, the species is invasive outside its native range. Perhaps, the idea was that if a species is invasive in one area then after introduction into another area, it is also likely to be invasive, but this does not explain anything about why it is invasive.

The putative "impact outcomes" were: modifications of the nutrient regime, formation of a monoculture, negative impacts of forestry, reduced native biodiversity and threat to/ loss of native species. These statements seem to be exaggerated. There is an absence of knowledge about modifications of the nutrient regime in this species. It is unlikely that the species could affect forestry. Reduction of native biodiversity and the threat to native species have not yet been proven conclusively. The "impact mechanisms" that were listed include competition – monopolizing the resources' pest and disease transmission and rapid growth. These statements are accurate to some extent. Small balsam is a very weak competitor and only in its seedling stage but it does not monopolize resources – nutrients, light or space. It does indeed show rapid growth. It can transmit some diseases; however, its pests and pathogens are very specific such as *Puccinia komarovii* and attack small balsam almost exclusively.

Based on knowledge that has been obtained about the history of invasions and the properties of the species, several schemes can be proposed to explain the pattern of an invasion by small balsam (Fig. 94-96).

Impatiens parviflora is found more frequently along forest paths and forest margins rather than inside forest interiors, which has been shown by many studies. As was postulated by Klimko and Piskorz (2003), a network of paths, roads, firebreaks, etc. – any type of artificial habitats of an anthropogenic origin – can be used by small balsam as migration routes into a forest. These habitats are less vegetated and have better light conditions than sites under tree canopies and therefore there is a greater chance for the long-distance dispersal for small balsam. Forest paths are used by forestry vehicles and equipment more frequently and therefore they are more trampled (Trepl 1984). It can be assumed that the rate of the spread of small balsam along a forest road network is faster than within the dense herbaceous ground flora under tree canopies (Fig. 94). The system of roads and paths also determines the direction of spread. At the beginning of an invasion, small balsam quickly penetrates the system of linear shaped man-made biotopes and simultaneously penetrates along the gradient forest road-forest interior where it runs more slowly.

Generally, the patches of individuals that grow along forest roads are denser and occupy larger areas. In some cases these populations are quite extended, as much as several hundreds of meters long. Kujawa-Pawlaczyk (1991) called them "ditch populations". Such populations were observed in the Silesian Upland and more rarely in the Jurassic Upland (Chmura 2004, unpublished). When a species enters into a non-forest habitat within a forest complex, i.e. cutting areas, forest glades, its abundance can increase.

Such a population can be the starting point for the further spread of the plant. Such a network of forest paths, cutting areas and forest glades creates an anthropogenic pathway for an invasion by *I. parviflora*, which is faster and more efficient for the spread and persistence of population. There is a natural pathway as well (Fig. 94). Windthrow fallen trees and coarse dead wood are present in the natural deciduous forests in lowlands due to natural disturbances. These create canopy gaps that facilitate an invasion by small balsam.

The rate of penetration within a forest interior is slowed down through natural pathways (Fig. 94). A population of small balsam can only become denser, more abundant and survive longer than several seasons only under the canopy gaps that are associated with fallen trees.

Long-distance dispersal is probably a few-fold lower and hindered. Only birds and mammals (roe deer, wild boars) can contribute to the propagation of *I. parviflora* within a forest interior.
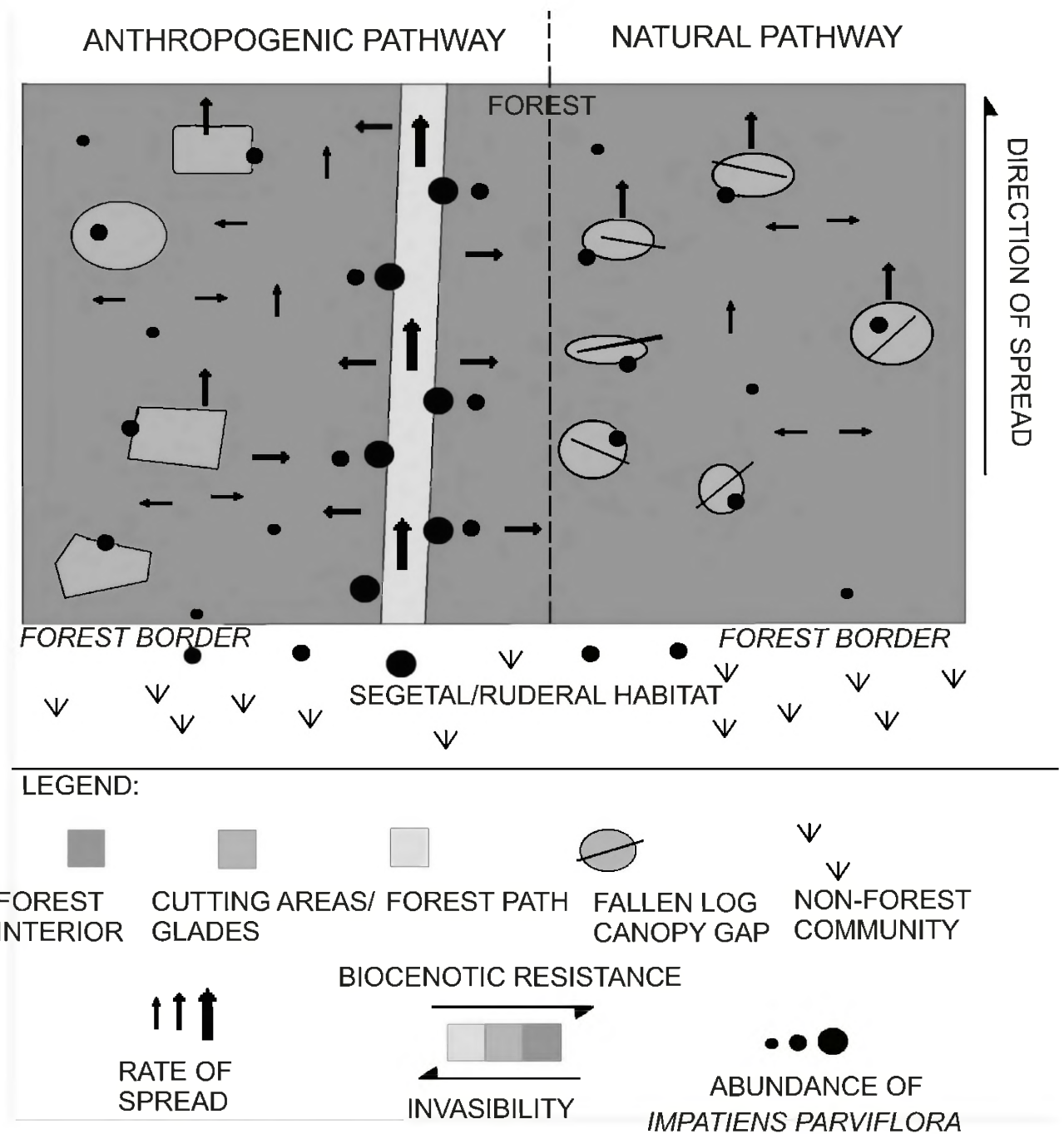
Fig. 94. Model of the association between the rate of the spread of *Impatiens parviflora* and the biocenotic resistance of vegetation and the type of habitat against the background of the spatial organization of disturbed and natural forests
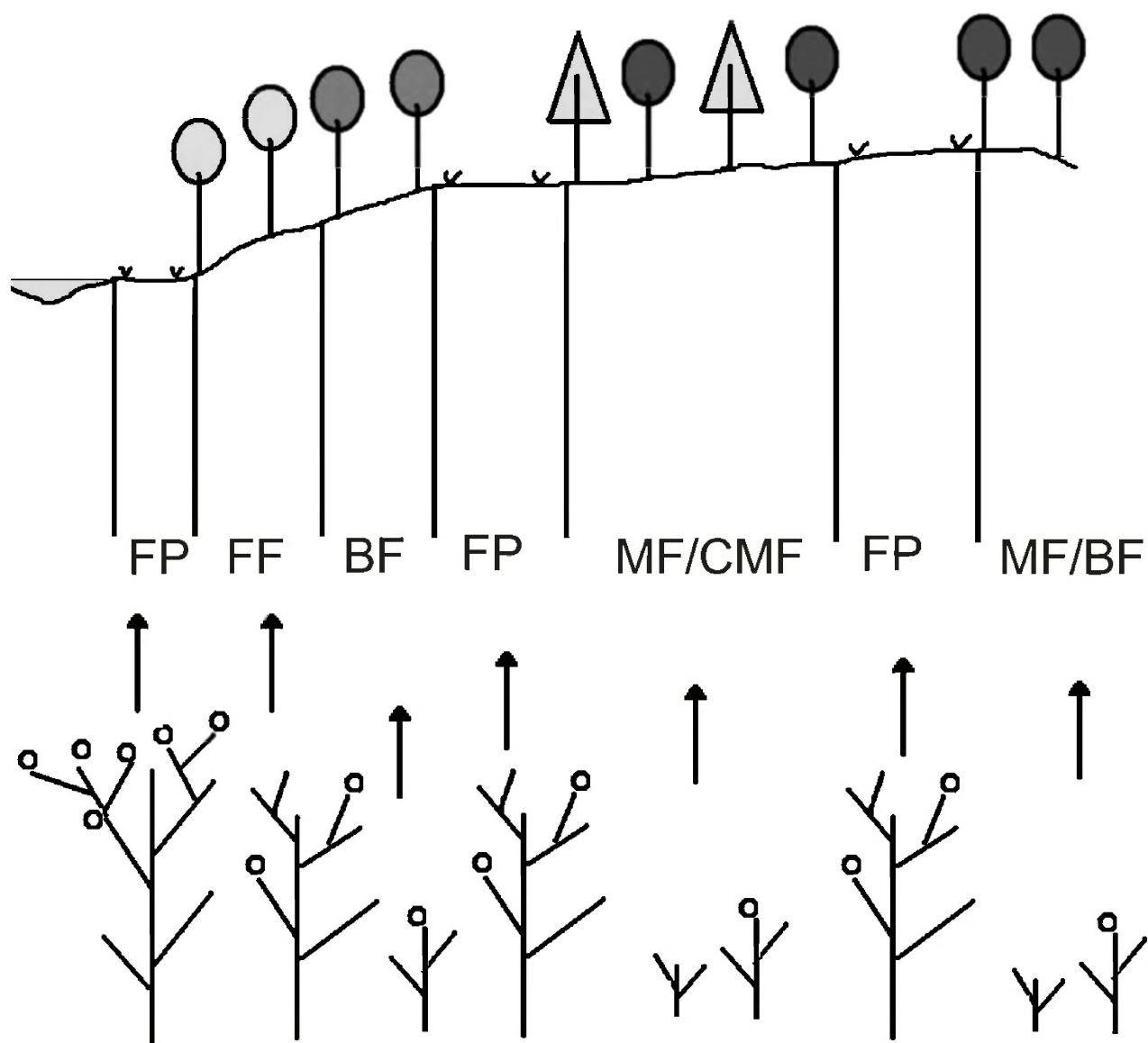
FP - Forest path, FF - Floodplain forest,
BF-Broad leaved forest, MF - Managed forest,
CMF - Coniferous mixed forest

Fig. 95. Differences in the size and fecundity of individuals of *Impatiens parviflora* according to the type of community/habitat

A common feature of both types of pathways is the greater abundance of populations that are growing on disturbed sites (roads and paths vs. canopy gaps and fallen logs), which can be called "disturbance populations". These patches of individuals are characterized not only by their abundance but also by other modified life history traits (Fig. 95).

Propagule input of
I. parviflora

Morphological
variation

Presence of AM
community

Presence of
natural
enemies

Presence of
pollinators

Zoopressure

+/-

+

+

+

-

+

Long
dispersal

+/-

+/-

Invasiveness

Human
activity

+/-

+

+

Unused resources

?

+

Invasion success

Disturbance

+

Habitat compability[1]

+

Invasibility

+

Input of resources

+

+

Biocenotic
resistance

-

Functional diversity

+

+

Species richness

+

+

Propagule input of
native taxa

Fig. 96. Model of the casual relationships between the factors and processes that influence species invasiveness and the invasibility components of the invasion success of *Impatiens parviflora*. Arrows indicate the direction of action; + increase, – decrease; ? no action or an unknown action, [1] – apart from favorable soil or substratum conditions, this includes beneficial (micro)climate conditions. Some ideas were incorporated from Rejmánek *et al.* (2005) but modified

These plants are usually taller and have more flowers and fruits; they also set more seeds. Their blooming phase starts earlier and sometimes lasts longer than that of individuals that grow in "forest interior populations". The propagule pressure of these disturbance populations is higher than that of forest interior populations. Moreover, it is more likely that disturbance populations will exhibit long-distance dispersal more often because plants are exposed to contact with more vectors (man and animals) in these habitats. Forest interior populations differ in life traits in their dependence on trophy (lower in mixed coniferous forests), light availability (lower in a dense, compact treestand of broad-leaved forests). The third factor is a disturbance that promotes a larger size and increased fecundity (Fig. 96).

The existence of both types of populations is similar to that of the dynamics of a metapopulation on a local scale. Owing to short-distance dispersal (up to 3.4 m Trepl 1984) by

autochory, the distances between populations of small balsam within one forest area are relatively long. The disturbance population can function as a source population because of a higher degree of propagule pressure and forest interior populations tend to be a sink population type, which are supplied by migrating individuals from disturbed sites. Klimko and Piskorz (2003) wrote that the "ability of *I. parviflora* to invade a continuous forest complex depends on the intra-population characteristics". While this is a true, it can be added that among the habitats in a given forest complex, a local metapopulation of *I. parviflora* always shows a high degree of morphological plasticity. Indeed, its ability to spread is dependent on the characteristics of plants, which depend on the forest complex and mosaic of habitats and microcosms that exist there. Plants differ in their size, fecundity and phenology along the gradients of nutrients, light conditions and space, which has been proven in many studies. Some environmental conditions are more suitable for plants of small balsam which responds through faster growth and a modified allocation of biomass. Its relatively high morphological plasticity, which also changes over time, as well as space are a major drivers of species invasiveness.

The criteria that relate to the ability to become invasive and to achieve invasion success generally belong to two categories – species invasiveness and a habitat's invasibility (Fig. 96). The first includes all of the biological characters that promote the spread and/or, competition, the measures of which are generally theoretically derived from the abundance of the population on the site and which are usually expressed in terms of cover or the degree of dominance. The ecological background of invasibility relates to disturbance, the availability of resources (nutrients and moisture) and interactions with resident biota (competition, mutualism and herbivory) (Richardson, Pyšek 2012). Propagule pressure in terms of intentional or unintentional introduction by humans is sometimes considered to be a third factor.

Some factors play a role at the beginning of invasion during the naturalization phase, while other factors influence the process of ongoing invasion (Kueffer *et al.* 2013). The environmental variables and biocenotic factors that currently influence invasions of *I. parviflora* are presented in figure 96. During the first phase of an invasion, the character and number of subsequent introductions are the most important for further spread. Close climate matching is also fundamental for progression along the continuum in a novel environment (Richardson, Pyšek 2012).

Among other pivotal issues, residence time enhances naturalization and the rate of propagation of the species as well. Residence time and all of the elements of propagule pressure, which encompass the quantity, quality, composition, rate and other details of the supply of propagules, are widely acknowledged as being positively associated with the "success'" of N introduced species (Richardson, Pyšek 2012). It is possible that alien species can be "forced" to be invasive

because of permanent frequent introductions. For instance, it was revealed and exemplified in Florida that the probability of plants becoming naturalized increased significantly with the number of years the plants were on sale as horticultural plants (Pemberton, Liu 2009). *Impatiens parviflora* is a case of a naturalized and invasive plant that was mainly introduced unintentionally (Trepl 1984).

Propagule pressure is one of the key phenomena. The higher the number of seeds that are released, the greater the probability of the establishment and founding of new populations. It is a stochastic process that is influenced by residence time (Richardson, Pyšek 2012). Residence time matters within the new invasive range of a nonnative species not only on a regional or global scale but also important on a local scale. The degree of invasion of small balsam within a forest complex depends on the residence time since the introduction on to the site. The model of invasion by *I. parviflora* (Fig. 96) does not take into account residence time because all of these processes occur over time. The main component that is associated with time is the continuous propagule pressure of small balsam and therefore only it is presented.

Due to natural intra-population variation, propagule pressure has an indirect impact on morphological variation and as a consequence, this results in morphological plasticity. Variations in the biological traits in a species are determined genetically. The environment, in turn, selects and causes the phenotypical responses of a species. The presence of various biotas (mutualists and enemies) facilitates or hampers an invasion of plants. Human activity and animals are responsible for long-distance dispersal. Some human actions can hinder the spread of a species. For instance, managed coniferous forests from which coarse dead wood is removed, are less vulnerable to invasion by small balsam than natural broad-leaved woods. A moderate level of climatic/environmental matching is essential to enable an introduced species to establish, survive and reproduce (Richardson, Pyšek 2012). Environmental factors remain fundamental during the further spread of the species. The interplay of the input of resources and disturbances along with habitat compatibility make habitats more vulnerable for the establishment, increase in abundance and further spread of the introduced species.

Biocenotic resistance in terms of native species cover, species richness and the participation of particular ecological groups (in the case of *I. parviflora*: tree seedlings, geophytes, plants of clonal growth) is an effective barrier that protects a habitat from invasion or that simply slows down this process.

5. Conclusions

- *Impatiens parviflora* DC is a species with a very high degree of morphological plasticity that is mainly induced by light availability followed by nutrient supply. This high degree of variation in the morphometric features of the plant is manifested by differences among the types of habitats/plant communities it occupies.

- It is a species that is rather a "passenger" than a "driver" of disturbances. In well-developed forest habitats, it penetrates sites that are unoccupied by other plants and utilizes any unused resources. In disturbed forest habitats, which have higher amounts of unused resources, it colonizes such sites with other species.

- It has the ability to occupy very diverse microhabitats, which is one of the most important aspects of its invasiveness. Despite the short seed dispersal spread of the species, it is very effective. The presence of plants in some types of substrata, e.g., hollows; bark of living trees and dead logs indicates the possibility of zoochorous spread.

- The competitive ability of small balsam in the herbaceous layer is a rather low. An increase or decrease in its abundance in the presence of other species, which was observed over time, is rather a consequence of a shift in its biotopic requirements. Biocenotic resistance (species richness and total species cover) are effective barriers and reduce the invasion success of the species.

- In specific microcosms (hollows, bark of living trees, dead logs, treefall disturbances), *I. parviflora* is the most frequent colonizer and perhaps it responds efficiently as a stress tolerator.

- Mutualistic interactions seem to support an invasion by small balsam. Arbuscular mycorrhization combined with some environmental factors is related to a higher robustness and fecundity of plants.

- The presence of *I. parviflora* in many openings and under canopy habitats promotes an extension of the seed production period because of shifts in the phenology of plants.

- A mosaic of disturbed (natural or man-made) and undisturbed habitats is a necessary factor for the existence of sustainable populations of the species under forest conditions. A population of small balsam in a forest complex exists as source-sink metapopulation. Source populations exist on disturbed sites (canopy gaps, forest margins) in which individuals are characterized by larger sizes and increased seed production. Forest interiors are habitats for sink populations that are typified by a lower morphological plasticity and ability of seed setting.

- The history of an invasion by *I. parviflora* in a specific area has an influence on the further process of the dynamics of the species. Invaded areas differ in the invasion level by *I. parviflora* and therefore the species increases in abundance on some sites while it declines on others.

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Appendix 1. Phytocoenotic spectrum of neophytes in forest communities of Silesian Upland. Constancy and median non-zero cover are included in the table. Only relevés with participation of neophytes are presented

Name of plant association	L-P	M-P	Q-P	C-P	PI	C-Q	T-C	L-F	EF	FU	FA	ZA	RA
Number of relevés in the table	80	8	128	16	11	31	94	36	19	12	28	17	5
Impatiens parviflora	I(3)	II(2)	III(13)	II(2)	V(63)	III(3)	IV(13)	III(3)	IV(3)	IV(3)	IV(3)	II(7)	III(13)
Acer negundo a	.	.	.	.	.	.	I(3)	.	.	.	.	.	.
Acer negundo b	.	.	I(2)	.	.	.	.	.	.	.	.	I(2)	.
Acer negundo c	.	.	.	.	.	.	I(2)	.	.	.	.	.	.
Digitalis purpurea	.	.	.	.	.	I(2)	.	.	.	.	.	.	.
Epilobium adenocaulon	.	.	.	.	.	I(2)	.	.	.	.	.	.	.
Erechtites hieracifolia	I(2)	.	.	.	.	.	.	.	.	.	.	.	.
Erigeron annuus	.	.	I(2)	.	.	.	.	.	.	I(13)	.	.	.
Galinsoga ciliata	.	.	.	.	.	I(2)	.	.	.	.	.	.	.
Galinsoga parviflora	.	.	.	.	.	.	I(2)	.	.	.	.	.	.
Impatiens glandulifera	.	.	.	I(2)	.	.	I(3)	.	.	.	.	.	.
Juncus tenuis	.	.	.	I(2)	.	.	.	.	.	.	.	.	.
Lupinus polyphyllus	I(3)	.	I(2)	.	.	.	.	.	.	.	I(3)	.	.
Oxalis fontana	.	I(3)	.	.	.	I(2)	I(2)	I(2)	.	.	.	.	.
Padus serotina a	I(13)	.	I(3)	.	I(38)	.	I(2)	.	.	.	I(13)	I(3)	I(13)
Padus serotina b	II(13)	II(13)	II(13)	I(13)	I(38)	I(8)	I(8)	I(3)	I(3)	.	I(7)	III(3)	I(13)
Padus serotina c	III(3)	III(2)	II(3)	I(2)	.	I(13)	I(3)	II(2)	I(2)	.	I(3)	II(2)	.
Quercus rubra a	I(13)	.	II(38)	III(3)	I(3)	II(8)	I(13)	II(3)	.	.	.	.	.
Quercus rubra b	II(3)	I(3)	II(3)	II(3)	I(13)	II(3)	I(3)	I(13)	I(8)	.	I(7)	I(2)	.
Quercus rubra c	III(2)	.	II(3)	II(2)	II(13)	II(2)	II(3)	II(3)	I(3)	.	I(2)	II(3)	.
Reynoutria japonica	I(3)	.	.	.	.	I(13)	.	.	I(13)	.	.	.	.
Robinia pseudacacia a	I(3)	.	I(2)	.	.	.	I(2)	.	.	I(2)	.	I(8)	.
Robinia pseudacacia b	I(3)	.	I(2)	.	.	.	.	.	.	.	.	I(8)	.
Robinia pseudacacia c	I(3)	.	I(3)	.	.	.	.	.	.	I(2)	.	I(2)	.
Solidago canadensis	.	.	I(2)	.	.	.	I(3)	.	.	.	I(3)	I(3)	.
Solidago gigantea	I(2)	.	I(3)	I(3)	I(3)	I(3)	I(13)	.	I(2)	.	I(13)	I(3)	.

Explanations: L-P- *Leucobryo-Pinetum*; M-P- *Molinio-Pinetum*; Q-P- *Querco roboris-Pinetum*; C-P- *Calamagrostio villosae-Pinetum*; PI anthropogenic community with *P. sylvestris*; C-Q – *Calamagrostio-Quercetum*; T-C – *Tilio-Carpinetum*; L-F- *Luzulo pilosae- Fagetum*; EF- *Fagenion*; F-U- *Ficario-Ulmetum*; F-A- *Fraxino-Alnetum*; ZA – anthropogenic community of *Querco-Fagetea* class; R-A- *Ribeso nigri-Alnetum*.

Appendix 2. Floristic diversity of accompanying species *Impatiens parviflora* in nature reserves in the Jurassic Upland (KC) and the Silesian Upland (SU). In the table percent percentage of occupied subplots by species are given. The order is given according to the decreasing frequency

Species	KC	SU	Species	KC	SU
Oxalis acetosella	23.73	7.68	Agrostis canina	0.03	0.45
Galeobdolon luteum	19.73	1.13	Ranunculus repens	0.57	0.00
Fagus sylvatica	15.00	3.71	Deschampsia caespitosa	0.00	0.42
Aegopodium podagraria	17.17	1.68	Moneses uniflora	0.00	0.39
Galium odoratum	13.57	1.95	Carex elongata	0.00	0.37
Carex brizoides	6.33	6.97	Anthriscus silvestris	0.43	0.00
Asarum europaeum	13.03	0.45	Brachypodium sylvaticum	0.40	0.03
Acer pseudoplatanus	13.10	0.26	Galium aparine	0.33	0.08
Viola reichenbachiana	11.37	1.26	Orthilia secunda	0.00	0.34
Vaccinium myrtillus	2.17	6.95	Padus serotina	0.00	0.34
Athyrium filix-femina	6.73	2.58	Primola elatior	0.43	0.00
Maianthemum bifolium	4.00	4.42	Cardamine amara	0.00	0.32
Hedera helix	9.20	0.00	Agrostis capillaris	0.00	0.29
Pulmonaria obscura	7.57	0.00	Crataegus monogyna	0.20	0.13
Mycelis muralis	5.50	1.08	Dentaria glandulosa	0.20	0.13
Pteridium aquilinum	0.00	4.76	Ranunculus lanuginosus	0.37	0.00
Quercus robur	2.07	3.11	Solanum dulcamara	0.00	0.29
Rubus idaeus	0.50	4.11	Tussilago farfara	0.37	0.00
Anemone nemorosa	4.33	0.97	Abies alba	0.00	0.26
Impatiens noli-tangere	5.10	0.34	Fraxinus excelsior	0.33	0.00
Urtica dioica	3.70	1.39	Myosotis palustris	0.33	0.00
Circaea lutetiana	3.90	0.66	Scirpus sylvaticus	0.00	0.26
Mercurialis perennis	4.13	0.39	Veronica chamaedrys	0.33	0.00
Sanicula europaea	4.63	0.00	Alnus glutinosa	0.03	0.21
Geranium robertianum	4.50	0.08	Anthoxanthum odoratum	0.00	0.24
Acer platanoides	4.33	0.18	Campanula trachelium	0.17	0.11
Rubus hirtus	2.03	1.97	Equisetum arvense	0.00	0.24
Sambucus nigra	4.50	0.03	Eupatorium cannabinum	0.00	0.24
Pinus sylvestris	0.10	3.47	Leucobryum glaucum d	0.00	0.24
Festuca gigantea	1.40	2.26	Campanula rapunculoides	0.27	0.00
Dryopteris filix-mas	1.80	1.89	Lycopus europeus	0.00	0.21
Galeopsis pubescens	3.67	0.34	Vaccinium vitis-idaea	0.00	0.21
Geum urbanum	3.60	0.37	Veronica officinalis	0.27	0.00
Convallaria majalis	0.07	2.71	Calamagrostis canescens	0.00	0.18
Trientalis europaea	0.03	2.63	Dicranella heteromalla d	0.23	0.00

Species	KC	SU	Species	KC	SU
Luzula pilosa	0.30	2.34	*Glyceria maxima*	0.00	0.18
Carpinus betulus	0.83	1.89	*Calamagrostis arundinacea*	0.00	0.16
Tilia cordata	0.10	2.29	*Epilobium montanum*	0.20	0.00
Sorbus aucuparia	1.57	1.11	*Juncus effusus*	0.00	0.16
Dryopteris carthusiana	1.20	1.37	*Pleurozium schreberi* d	0.00	0.16
Melica nutans	2.10	0.61	*Quercus petraea*	0.20	0.00
Ajuga reptans	2.17	0.53	*Rhamnus catharticus*	0.20	0.00
Carex sylvatica	2.33	0.39	*Melampyrum nemorosum*	0.00	0.13
Geranium phaeum	2.77	0.00	*Poa trivialis*	0.00	0.13
Stachys sylvatica	2.50	0.18	*Veratrum lobelianum*	0.17	0.00
Deschampsia flexuosa	0.00	2.08	*Acer campestre*	0.13	0.00
Chaerophyllum aromaticum	2.47	0.00	*Galeopsis speciosa*	0.00	0.11
Poa nemoralis	1.70	0.47	*Lonicera xylosteum*	0.13	0.00
Allaria officinalis	2.00	0.00	*Monotropa hypopitys*	0.13	0.00
Euonymus europaeus	1.77	0.11	*Padus avium*	0.13	0.00
Fragaria vesca	0.03	1.47	*Senecio rivularis*	0.00	0.11
Rubus caesius	0.00	1.50	*Viola mirabilis*	0.13	0.00
Cruciata glabra	1.57	0.24	*Alnus incana*	0.00	0.08
Epipactis helleborine	1.83	0.00	*Campanula persicifolia*	0.10	0.00
Paris quadrifolia	1.13	0.50	*Dactylis glomerata*	0.00	0.08
Scrophularia nodosa	1.53	0.11	*Daphne mezereum*	0.10	0.00
Hieracium murorum	1.33	0.13	*Lamium purpureum*	0.00	0.08
Ulmus glabra	1.47	0.00	*Plantago major*	0.00	0.08
Calamagrostis epigejos	0.00	1.05	*Poa annua*	0.00	0.08
Picea abies	0.00	1.05	*Pyrola chlorantha*	0.00	0.08
Ribes nigrum	1.07	0.16	*Salix cinerea*	0.00	0.08
Quercus rubra c	0.00	0.95	*Taraxacum officinale*	0.00	0.08
Chrysosplenium alternifolium	1.17	0.00	*Cirsium arvense*	0.07	0.00
Lysimachia vulgaris	0.00	0.89	*Equisetum fluviatile*	0.00	0.05
Populus tremula	0.00	0.87	*Euphorbia amygdaloides*	0.00	0.05
Actaea spicata	1.07	0.00	*Gymnocarpium dryopteris*	0.00	0.05
Chaerophyllum hirsutum	0.00	0.84	*Humulus lupulus*	0.00	0.05
Stellaria holostea	0.27	0.63	*Luzula luzuloides*	0.07	0.00
Hepatica nobilis	0.73	0.18	*Melandrium album*	0.07	0.00
Milium effusum	0.13	0.66	*Oxalis stricta*	0.07	0.00
Glechoma hederacea	0.43	0.39	*Viburnum opulus*	0.07	0.00
Polytrichastrum formosum	0.93	0.00	*Aconitum moldavicum*	0.03	0.00
Astrantia major	0.73	0.13	*Alium ursinum*	0.03	0.00
Frangula alnus	0.00	0.71	*Cirsium palustre*	0.00	0.03

Species	KC	SU	Species	KC	SU
Ficaria verna	0.87	0.00	*Equisetum palustre*	0.00	0.03
Lamium maculatum	0.80	0.00	*Holcus lanatus*	0.00	0.03
Lilium martagon	0.80	0.00	*Knautia arvensis*	0.03	0.00
Lysimachia nummularis	0.77	0.00	*Lamium album*	0.03	0.00
Poa palustris	0.77	0.00	*Lapsana communis*	0.03	0.00
Lathyrus vernus	0.73	0.00	*Lathyrus niger*	0.03	0.00
Betula pendula	0.00	0.55	*Orthodicranum montanum*	0.03	0.00
Corylus avellana	0.03	0.53	*Polygonatum verticillatum*	0.03	0.00
Polygonatum multiflorum	0.40	0.24	*Sambucus racemosa*	0.00	0.03
Rubus plicatus	0.00	0.50	*Viola palustris*	0.00	0.03
Senecio nemorensis	0.10	0.42			

Appendix 3. Frequency of species accompanying *I. parviflora* in microhabitats associated with coarse woody debris. Abbreviations: ANL – area near log, H – hollow, LUC – logs under canopies, LUCO – logs under canopy openings, RP – root plate, S – snag, TFD – treefall disturbance, **TF – Total frequency**

	ANL	H	LUC	LUCO	RP	S	TFD	**TF**
N (number of species)	14(19)	3(5)	15(6)	20(13)	26(32)	20(21)	12(28)	**121**
Acer platanoides	4	0	0	0	0	0	1	**5**
Acer pseudoplatanus	1	0	0	0	0	0	1	**2**
Aegopodium podagraria	2	0	0	0	3	1	1	**7**
Ajuga reptans	1	0	0	0	3	1	0	**5**
Anemone nemorosa	1	0	0	0	1	0	0	**2**
Asplenium sp	0	1	0	0	0	0	0	**1**
Athyrium felix-femina	0	0	0	0	3	1	2	**6**
Betula pendula seedling	0	0	1	0	0	0	0	**1**
Brachypodium sylvaticum	1	0	0	0	2	0	0	**3**
Carex brizoides	0	0	0	0	0	1	0	**1**
Carex digitata	0	0	0	0	1	0	0	**1**
Carex silvatica	1	0	0	0	0	1	0	**2**
Chamaenerion angustifolium	0	0	0	0	3	0	0	**3**
Chelidonium majus	0	0	0	0	1	0	1	**2**
Circaea lutetiana	3	0	0	0	1	1	2	**7**
Convallaria maialis	0	0	0	0	2	0	0	**2**
Cruciata glabra	1	0	0	0	3	0	1	**5**
Dryopteris sp.	0	0	1	1	0	1	2	**5**
Epipactis helleborine	1	0	0	0	0	0	0	**1**
Eupatorium cannabinum	0	0	0	0	0	1	0	**1**
Euphorbia cyparissias	0	0	0	0	1	0	0	**1**
Fagus sylvatica	7	0	2	9	8	3	6	**35**
Galeobdolon luteum	0	0	0	0	1	0	1	**2**
Galeopsis pubescens	0	0	0	1	0	1	1	**3**
Galium odoratum	9	0	2	2	6	4	2	**25**
Geranium robertianum	0	0	0	1	2	0	4	**7**
Hedera helix	1	0	0	1	1	1	1	**5**
Impatiens parviflora	13	3	3	9	18	12	12	**70**
Lathyrus vernus	1	0	0	1	0	0	1	**3**
Luzula pilosa	1	0	0	0	1	1	0	**3**
Maianthemum bifolium	0	0	0	0	1	0	1	**2**
Melica nutans	1	0	0	0	0	2	1	**4**
Mercurialis perennis	0	0	2	8	5	2	2	**19**
Moehringia trinervia	0	2	0	0	0	1	0	**3**
Mycelis muralis	2	0	0	1	3	2	5	**13**
Pinus sylvestris	0	0	0	0	1	0	0	**1**
Poa nemoralis	1	0	0	1	3	2	2	**9**
Rubus sp.	0	0	0	0	2	4	1	**7**
Sambucus nigra	0	2	0	0	1	0	1	**4**
Sambucus racemosa	0	0	0	0	1	0	0	**1**
Solidago canadensis	0	0	0	0	1	0	0	**1**
Taraxacum officinale	0	0	0	1	4	0	4	**9**
Tussilago farfara	0	0	0	0	3	0	1	**4**

	ANL	H	LUC	LUCO	RP	S	TFD	**TF**
Urtica dioica	0	0	0	0	0	0	1	**1**
Veronica chamaedrys	0	0	0	0	0	0	1	**1**
Veronica officinalis	0	0	0	0	2	0	0	**2**
Viola reichenbachiana	0	1	0	1	2	2	2	**8**

Streszczenie (Polish summary)

Damian Chmura

Biologia i ekologia inwazji *Impatiens parviflora* DC na naturalnych i połnaturalnych siedliskach

W ostatnich dekadach byliśmy świadkami narodzin nowej dziedziny w obrębie nauk biologicznych – ekologii inwazji. Zjawisko rozprzestrzeniania się i zadamawiania obcych gatunków w nowej ojczyźnie stanowi, jako drugie po niszczeniu siedlisk, największe zagrożenie dla rodzimej różnorodności biotycznej. Stąd też nie dziwi zainteresowanie zagadnieniem rozprzestrzeniania się gatunków obcych u botaników, zoologów, ekologów jak i praktyków ochrony przyrody.

Niecierpek drobnokwiatowy *Impatiens parviflora* DC, rodzimy dla Wschodniej Azji we florze Polski ma status kenofita (holoagriofita). Można go uznać za „prawdziwie" inwazyjny gatunek obcego pochodzenia, ponieważ od momentu introdukcji proces jego rozprzestrzeniania się, zadamawiania przebiegał niemalże w sposób spontaniczny bez udziału człowieka. Obecnie to gatunek szeroko rozpowszechniony w lasach, wzdłuż dróg leśnych i na siedliskach ruderalnych.

Jednakże opinie co do wpływu tego gatunku na rodzimą florę, pewne aspekty biologii, ekologii, które mają go czynić skuteczną rośliną inwazyjną są podzielone. Doniesienia z różnych części Europy przedstawiają odmienne a czasem przeciwstawne wyniki badań.

Głównym celem badań miało być podsumowanie i przedyskutowanie mechanizmów inwazji niecierpka drobnokwiatowego w oparciu o wyniki własne i doświadczenia innych autorów.

Badania w niniejszej pracy mieszczą się w zakresie ekologii populacji, ekologii gatunku, fitosocjologii, ekologii zbiorowisk roślinnych i biocenologii. Studia nad gatunkiem przeprowadzone były w latach 2005-2012 lecz użyty materiał fitosocjologiczny pochodzi z okresu 1998-2012 (485 zdjęć). Prace terenowe wykonano na obszarze Wyżyny Śląskiej oraz na Wyżynie (Jurze) Krakowsko-Częstochowskiej. W tych dwóch mezoregionach, na terenie wybranych rezerwatów przyrody, założono łącznie 68 powierzchni badawczych o boku 10 m x 10 m podzielonych na 100 poletek w różnych zbiorowiskach leśnych celem badań nad ekologią zbiorowisk roślinnych z udziałem niecierpka. Na 10 z nich później prowadzono 8-letnie obserwacje. Dokonano również obserwacji na kilkunastu typach podłoży głównie związanych z różnym typem martwego drewna, gdzie śledzono losy oznakowanych osobników. Materiał (nasiona) oprócz wyżej wymienionych regionów pozyskano także z obszaru Węgier do badań nad biologią kiełkowania. Pobrano 30 prób do badań mikologicznych oraz ponad 150 prób gleby. Przeprowadzono badania morfologiczne, fenologiczne, glebowe, zbadano cechy historii życia *life history traits*, mykologiczne, fitosocjologiczne oraz długoterminowe badania ekologiczne. Wyniki prac terenowych oraz laboratoryjnych poddano różnym analizom statystycznym.

Potwierdzono, że *Impatiens parviflora* jest gatunkiem o wysokiej plastyczności morfologicznej, która ma związek z dużą dostępnością światła i nutrientów w podłożu. To wysokie zróżnicowanie utrzymuje się w różnicach w cechach morfometrycznych między zbiorowiskami i typami siedlisk, w których gatunek się pojawia.

Gatunek jest raczej beneficjentem (ang. *passenger*) niż czynnikiem sprawczym zaburzeń (ang. *driver*). W dobrze zachowanych leśnych siedliskach wykorzystuje wolną przestrzeń i zasoby nieużytkowane przez inne rosliny. W bardziej zaburzonych leśnych siedliskach kolonizuje takie miejsca z innymi gatunkami.

Roślina ta ma wielką zdolność zasiedlania bardzo różnorodnych mikrosiedlisk, co jest jednym z najważniejszych aspektów jej inwazyjności. Pomimo krótkodystansowej dyspersji wynikającej z autochorii, rozprzestrzenianie się niecierpka jest bardzo efektywne.

Obecność osobników niecierpka na takich siedliskach jak dziuple, kora żywych drzew świadczy o możliwościach zoochorii głównie przez ptaki.

Zdolność do konkurencji u tego gatunku jest niewielka zwłaszcza w warunkach warstwy runa. Wzrost lub zmniejszenie się udziału niecierpka w obecności innych gatunków jest raczej efektem różnic w wymaganiach siedliskowych niż mechanizmów konkurencji. Biocenotyczna odporność (bogactwo gatunkowe, pokrycie roślin) jest skuteczną barierą uniemożliwiającą lub redukującą sukces inwazji tego gatunku. W pewnych mikrosiedliskach (dziuple, kora żywych i martwych drzew, kłody, dołki powykrotowe) *I. parviflora* jest najczęstszym kolonizatorem i nalepiej toleruje stres środowiskowy spośród wszystkich obecnych gatunków roślin naczyniowych.

Interakcje mutualistyczne wydają się sprzyjać inwazji tego gatunku. Mikoryza arbuskularna w powiązaniu z pewnymi czynnikami siedliskowymi występuje u największych i najpłodniejszych osobników.

Obecność *I. parviflora* pod lukami w drzewostanie i pod okapem drzew powoduje wydłużenie czasu produkcji nasion wskutek przesunięcia się faz fenologicznych.

Mozaika zaburzonych (naturalnie i antropogenicznie) i niezaburzonych siedlisk jest koniecznym czynnikiem dla występowania trwałych populacji w warunkach leśnych. Populacja niecierpka drobnokwiatowego w leśnym kompleksie egzystuje jako metapopulacja typu „źródło-ujście". Populacje typu źródła występują na miejscach zaburzonych (luki, obrzeża lasu), w których osobniki charakteryzują się większymi rozmiarami i zwiększoną produkcją nasion. Z kolei siedliska typowo leśne, niezaburzone, tj.wnętrza lasu są siedliskami dla populacji typu ujście, gdzie rośliny odznaczają się mniejszą plastycznością morfologiczną i produkcją nasion.

Historia inwazji *I. parviflora* w danym miejscu ma wpływ na dalszą dynamikę tego gatunku. Obszary występowania gatunku różnią się stopniem inwazji stąd też można zaobserwować wzrost udziału niecierpka drobnokwiatowego w niektórych miejscach a w innych jego wycofywanie się.