

Alien plant species in secondary succession

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Abstract: The behaviour of geographically alien plants in the course of secondary succession on an abandoned field and an unmown meadow in the Experimental Garden of BGS was analysed. Amongst 226 species found on the abandoned field were: 36 archaeophytes and 31 kenophytes. Over 50% of the archaeophytes retreated after six years of observation, and their cover decreased from 20% to 2%. Only vetches (*Vicia angustifolia*, *V. hirsuta*, *V. tetrasperma*) thrived for longer on the plot. The cover of kenophytes decreased from 4% to zero in fourth year of observation and was insignificant up to 19-th year of observation. The first woody kenophyte, *Pinus strobus*, emerged in 15-th year of observation. In recent years the cover of kenophytes increased to 3%. At the moment *Acer pseudoplatanus*, *Crataegus* sp. and *Padus serotina* have the highest frequency amongst woody aliens in the herb layer. Ten kenophytes entered the shrub layer, although their cover is still negligible. On the unmown meadow amongst 198 taxa were 27 archaeophytes and 24 kenophytes. The number of archaeophytes fell from 24 in the first year of observation to 5 in the sixth, and cover from 4% to less than 1%. Archaeophytes were seen for the last time in 34-th year of observation. The cover of kenophytes fell from less than 1% to almost zero in the third year. Since 19-th year of observation the cover of kenophytes in the herb layer has been rising, recently reaching about 2%. The first woody kenophyte, *Malus domestica*, was established in third year of observation. Up to now 7 kenophytes have entered the shrub layer. Their cover recently reached about 5%. In 15-th year of observation *Malus*

domestica, and in 29-th year *Tilia platyphyllos* entered the tree layer. Their cover recently reached about 10%. The different behaviour of archaeophytes and kenophytes is, at least partially, the result of the prevalence of different ecological and biological peculiarities (e.g. life forms) of these groups of species.

Keywords: abandoned field, anthropophytes, long-term study, non-native species, unmown meadow, Białowieża Forest, Poland

Introduction

Elimination of land from agricultural use (i.e. ploughing, mowing and grazing) triggers secondary succession, leading in our climatic zone to the formation of secondary forest phytocenoses (FALIŃSKI 1986, 1988; FALIŃSKA 2003). Forest return on abandoned fields is a common ecological process observed today in the European landscape, and the restoration of forest communities after their destruction is one of the most frequently analysed problems in studies on vegetation dynamics (BOMANOWSKA & KIEDRZYŃSKI 2011, and the literature cited therein). Conducted research showed that several hundred years may be needed for spontaneous forest return (FALIŃSKI 1986; ADAMOWSKI & BOMANOWSKA 2011a), and this process does not always lead to the recovery of the former forest community (GRINN-GOFRON 2007; ŁASKA 2007). Many authors (FALIŃSKI 1998; FIKE & NIERING 1999; REJMÁNEK 1999; MEINERS et al. 2001, 2002; BARABASZ-KRASNY 2002; WĘGRZYNEK et al. 2005; BANASIAK & MEINERS 2009; TOGNETTI et al. 2010; BALCERKIEWICZ & PAWLAK 2011 and others) also draw attention to the fact that disturbed post-agricultural habitats are susceptible to invasion by non-native species (anthropophytes). Conducted studies showed that numerous alien plant species may contribute to community dynamics at different stages of succession; some of them are able to accelerate, slow down or change the process's course (FIKE & NIERING 1999; MEINERS et al. 2001; YURKONIS & MEINERS 2004; BANASIAK & MEINERS 2009). Despite this widely observed tendency few long-term studies have focused on non-native plant dynamics during succession (FIKE & NIERING 1999; MEINERS et al. 2001, 2002; MEINERS 2007; BANASIAK & MEINERS 2009; TOGNETTI et al. 2010; BALCERKIEWICZ & PAWLAK 2011).

Detailed observations conducted on abandoned farmland in Białowieża Forest, as well as long term studies on permanent experimental plots (ADAMOWSKI et al. 2002; MĘDRZYCKI 2002; PABJANEK 2003; ADAMOWSKI & BOMANOWSKA 2007, 2008; BOMANOWSKA & ADAMOWSKI 2009) confirmed the encroachment of numerous non-native taxa into the process of secondary succession.

The aim of the study was the analysis of the behaviour of geographically alien plants in the course of secondary succession on an abandoned field and an unmown meadow, particularly: i) comparison of roles in the process of secondary succession of two different groups of anthropophytes, namely archaeophytes and kenophytes; ii) prediction of further share of non-native taxa in secondary succession.

Material and methods

The Experimental Ecological Garden of the Białowieża Geobotanical Station (BGS) of Warsaw University is located in the central part of the Białowieża Clearing, in subcontinental oak-hornbeam forest *Tilio-Carpinetum typicum* habitat. This area had been in agricultural use from the late 17th century, up to the moment of its acquisition by the BGS (FALIŃSKI 1986). The Garden came into existence in 1974 on an area of 1.2 ha in the location of a former arable field and mown meadow. The last cultivations, in 1973, were potatoes and cabbage, which were accompanied by a segetal community, *Echinochloo-Setarietum*, while the meadow was described as belonging to the *Arrhenatheretum elatioris* association (FALIŃSKI 1986, 2002). Two sectors were selected for long-term observations on the initiation and progress of secondary succession on the abandoned field (sector C) and the unmown meadow (sector E) under monitored conditions, each with an area of 400 m². Both permanent study areas are divided into 22 basal plots, each with an area of 10 m² (6.25 m x 1.6 m), separated by paths with a width of 30 cm. The plots are surrounded by an isolating belt which is 120-220 cm wide. A detailed description of the site of the experiment, its habitat conditions and the treatments used can be found in earlier papers by FALIŃSKI (1986, 2002), as well as ADAMOWSKI & BOMANOWSKA (2011a).

The founder of the project and its long term coordinator was J. B. FALIŃSKI. Regular observations have been conducted (since 1974) once a year, around the end of June and the beginning of July. Until 1995 all the observations were carried out by A. U. Warcholińska, and are continued at present by the authors of this paper. The following features were recorded: overall species composition, structure of the plant community, appearance of seedlings and juvenile individuals of woody species. To fulfil this goal, a phytosociological relevé was recorded from each basal plot by the classical Braun-Blanquet method, while cover for each species was assessed in the numerical scale of Braun-Blanquet (1964) and in the decimal scale of Londo (1976). Since 2000 the occurrence of spring geophytes has been recorded at the end of April or the beginning of May.

The data used in this work were collated in the BGS archive and obtained from sector C (former arable field) and sector E (former mown meadow). Data from 17 observation plots were included in the analysis (=170m²) because in the five remaining ones (C1-C3, C12 and C13 in Sector C; E10, E11 and E20-E22 in Sector E) since 1984 plants have been mown each year after observation and the biomass removed from the plot. The total cover of plants was calculated from the cover index values for individual species, estimated using the Londo scale. The following conversion factors for the Londo scale were adopted: 0.1 – 0.5% cover, 0.2 – 2%, 0.4 – 5%, 1 – 10%, 2 – 20%, 3 – 30%, etc.

In our work the presence, frequency and cover of geographically non-native plant taxa were analysed. The study implements the geographical-historical classification of flora following the classification proposed by KORNAŚ (1977) and supplemented by MIREK (1981) and JACKOWIAK (1990). The status of anthropophytes was determined according to the studies by ZAJĄC (1979), SOKOŁOWSKI (1995), ADAMOWSKI et al. (2002), MIREK et al. (2002), TOKARSKA-

GUZIK (2005) and ZAJĄC & ZAJĄC (2011), although the degree of naturalization of alien taxa was related to local conditions. The detailed analysis concerned established alien species (metaphytes), represented by archaeophytes and kenophytes, which have no natural sites of occurrence in the Białowieża Forest region. All data given on figures concern these two groups of taxa.

The Latin names of vascular flora were used according to MIREK et al. (2002).

Results

1. Amongst total 226 vascular plant taxa found in whole (38) years of observation on the abandoned field were 67 metaphytes (established alien species): 36 archaeophytes and 31 kenophytes (24 woody, 7 herbaceous), which is almost 30% of all taxa. On the unmown meadow amongst 198 species found were 27 archaeophytes and 24 kenophytes (20 woody, 4 herbaceous), which is almost 26% of all taxa.
2. In individual years 6 to 36 geographically alien plant taxa were observed on the abandoned field, which is 7.5 to almost 39% of all taxa found in a particular year. At the beginning of our study the number of alien taxa diminished quickly (Fig. 1a), reaching a minimum in 13-th year of observation. Later, the number of anthropophytes started to rise gradually, in the last years reaching 19-20 taxa. On the unmown meadow 4 to 26 anthropophytes were found, which is 6 to 26% of all taxa found in a particular year (Fig. 1b). As in the abandoned field, this number went down, with minima in ninth year of observation and between 17-th and 20-th year of observation. In the last years the number of anthropophytes reached 15-18 taxa.
3. On average fewer than 3 to 18 anthropophytes per basal plot were found on the abandoned field in particular years (Fig. 2a). This number was falling at the beginning of our study, reaching minima in sixth year of observation and 17-th year of observation; since then we have observed a slow rise in the frequency of anthropophytes. On the unmown meadow the frequency of all anthropophytes oscillated between 0.5 and 8 per basal plot in particular years (Fig. 2b). As in the abandoned field, it was falling at the beginning of our study, reaching minima in ninth year of observation and 18-th year of observation. Recently the frequency of anthropophytes has been about 3.5 alien taxa per basal plot.
4. Total cover of anthropophytes was almost 24% in first year of observation on the abandoned field. The share of anthropophytes quickly diminished till sixth year of observation and changed irregularly till 23-rd year of observation. In the last years the total cover of anthropophytes fluctuated around 3% (Fig. 3a). On the unmown meadow the total cover of anthropophytes diminished from 4% in first year of observation to 0.3% in ninth year of observation. After the second minimum in 18-th year of observation this value has been gradually rising (Fig. 3b).

5. The number of archaeophytes on the abandoned field fell from 32 in first year of observation to 9 in sixth year of observation and 3 (*Vicia angustifolia* L., *V. hirsuta* (L.) Gray, *V. tetrasperma* (L.) Schreb.; Fig. 1a) in 36-th year of observation, and their cover from 20% to less than 1% in the same time (Fig. 3a). On the unmown meadow the number of archaeophytes fell from 24 in first year of observation to 5 in sixth year of observation (Fig. 1b), and cover from 4% to less than 1% in the same time (Fig. 3b). Archaeophytes were seen there for the last time in 34-th year of observation.
6. The share of kenophytes on the abandoned field diminished at the beginning of our study (from 4 taxa and about 4% of cover to 0 in fourth year of observation); between fifth and nineteenth year of observation it was negligible (0-6 taxa, less than 0.3% of cover); later it started to rise gradually (to 15-17 taxa and more than 3% of cover in the last years; Fig. 1a and 3a). On the unmown meadow the cover of kenophytes fell from less than 1% almost to zero in third year of observation. Since 19-th year of observation the number of taxa and the cover value of kenophytes in the ground layer has been rising, recently reaching 15-18 taxa and about 2% (Fig. 1b and 3b).
7. The number of taxa and the cover value amongst herbaceous kenophytes on the abandoned field were falling even faster than amongst archaeophytes (Fig. 1a and 3a). Only one herbaceous kenophyte, *Conyza canadensis* (L.) Cronquist, had significant cover in first year of observation. On the unmown meadow the share of herbaceous kenophytes is negligible all the time (0-2 taxa, less than 1% of cover; Fig. 1b and 3b). *Rumex confertus* Willd. has been observed yearly since 15-th year of observation.
8. The first woody kenophyte on the abandoned field (*Pinus strobus* L.) emerged in 15-th year of observation. On the unmown meadow *Malus domestica* Borkh. was established in third year of observation.
9. The number of taxa and the cover value of woody kenophytes on the abandoned field rapidly increased between 17-th and 20-th year of observation, and they are still slowly growing (Fig. 1a and 3a). On the unmown meadow these changes were more irregular and gradual (Fig. 1b and 3b).
10. Amongst woody kenophytes *Crataegus* sp., *Acer pseudoplatanus* L. and *Padus serotina* (Ehrh.) Borkh. have recently had the highest frequency on the abandoned field; on the unmown meadow: *Crataegus* sp. and *Malus domestica*.
11. Ten kenophytes entered the shrub layer on the abandoned field, although their cover reached 1% only recently (Fig. 4a). On the unmown meadow seven kenophytes were found in the shrub layer, their cover reaching about 5% (Fig. 4b).
12. No one kenophyte entered the tree layer on the abandoned field. On the unmown meadow *Malus domestica* and *Tilia platyphyllos* Scop. entered the tree layer. Their cover recently reached about 10% (Fig. 5).

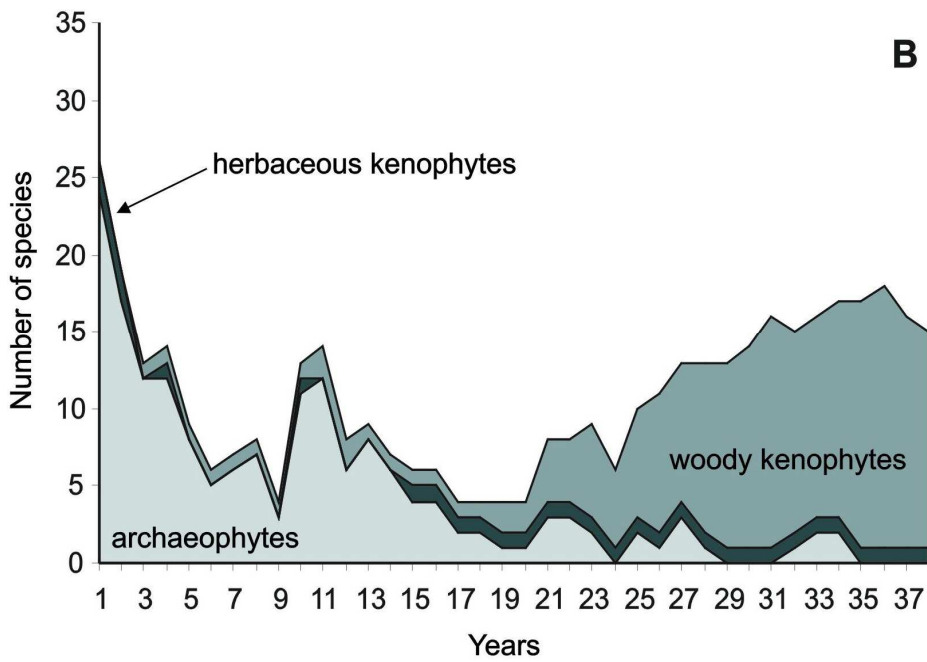
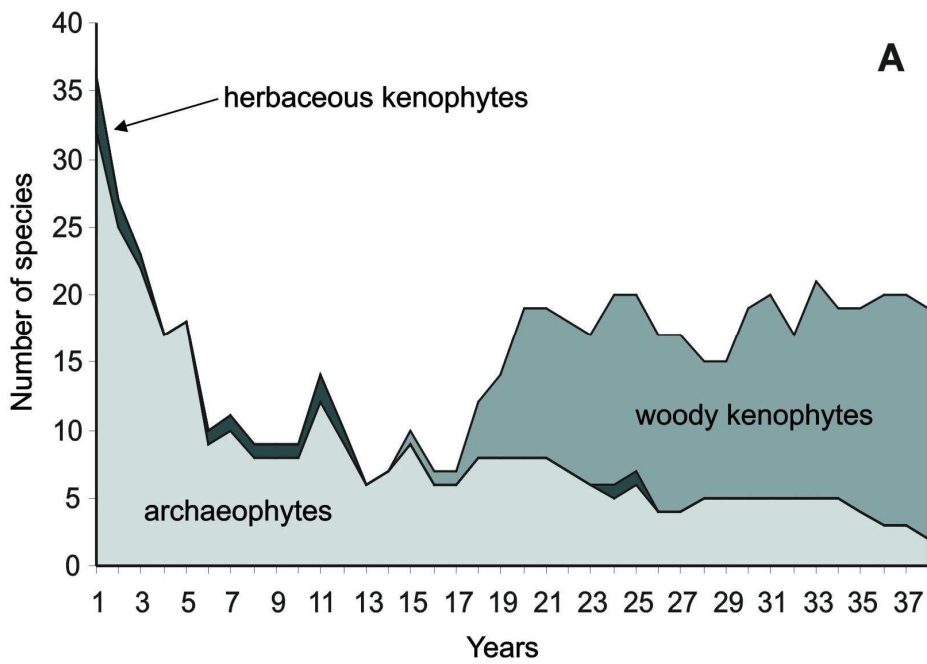


Fig. 1. Overall number of non-native taxa in the herb layer in the course of secondary succession. A - abandoned field, B - unmown meadow

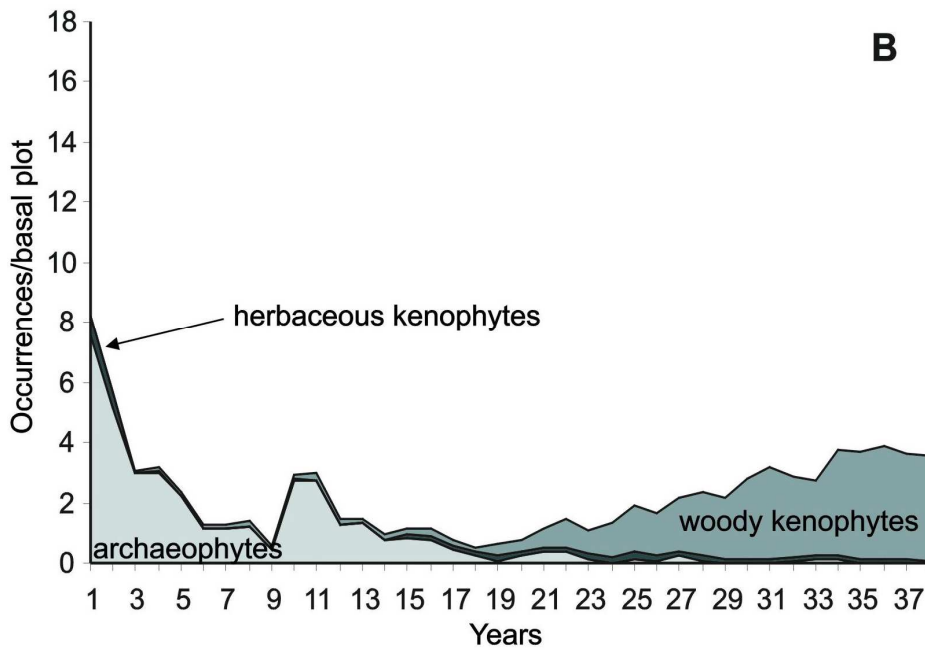
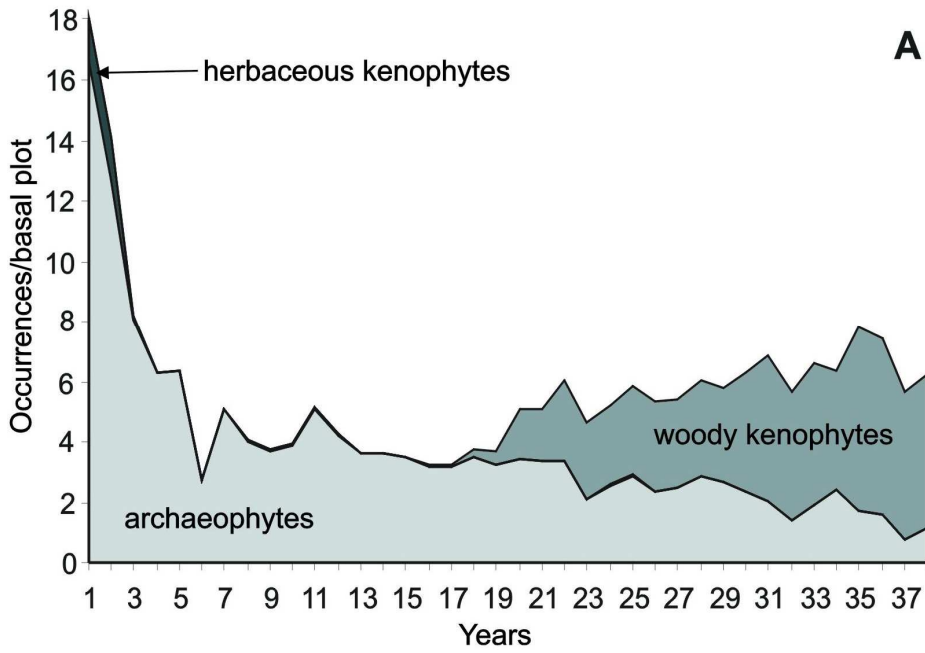


Fig. 2. Average number of non-native taxa in the herb layer in the course of secondary succession. A - abandoned field, B - unmown meadow

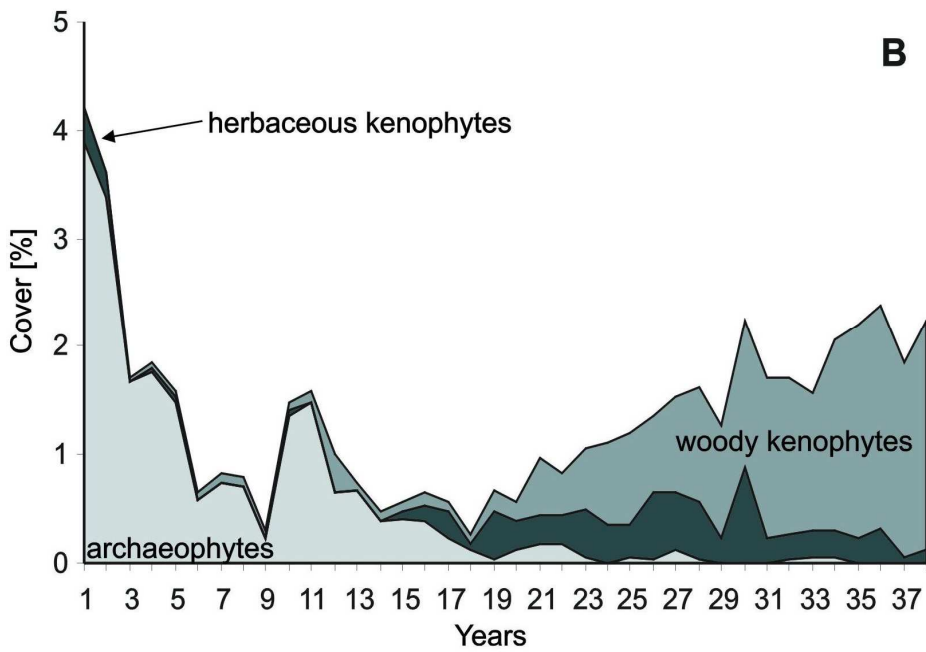
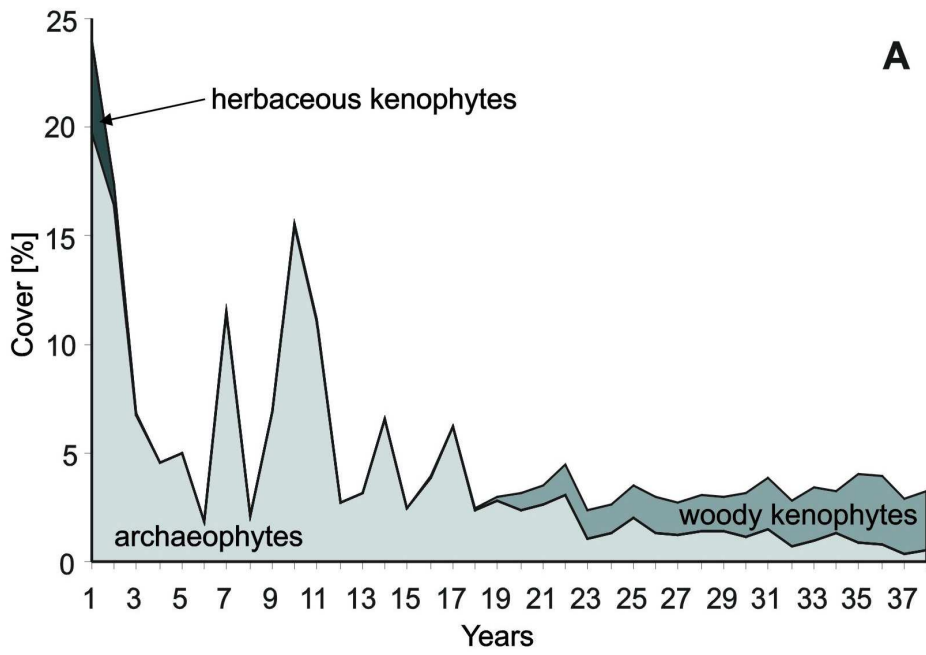


Fig. 3. Total cover of non-native taxa in the herb layer in the course of secondary succession. A - abandoned field, B - unmown meadow

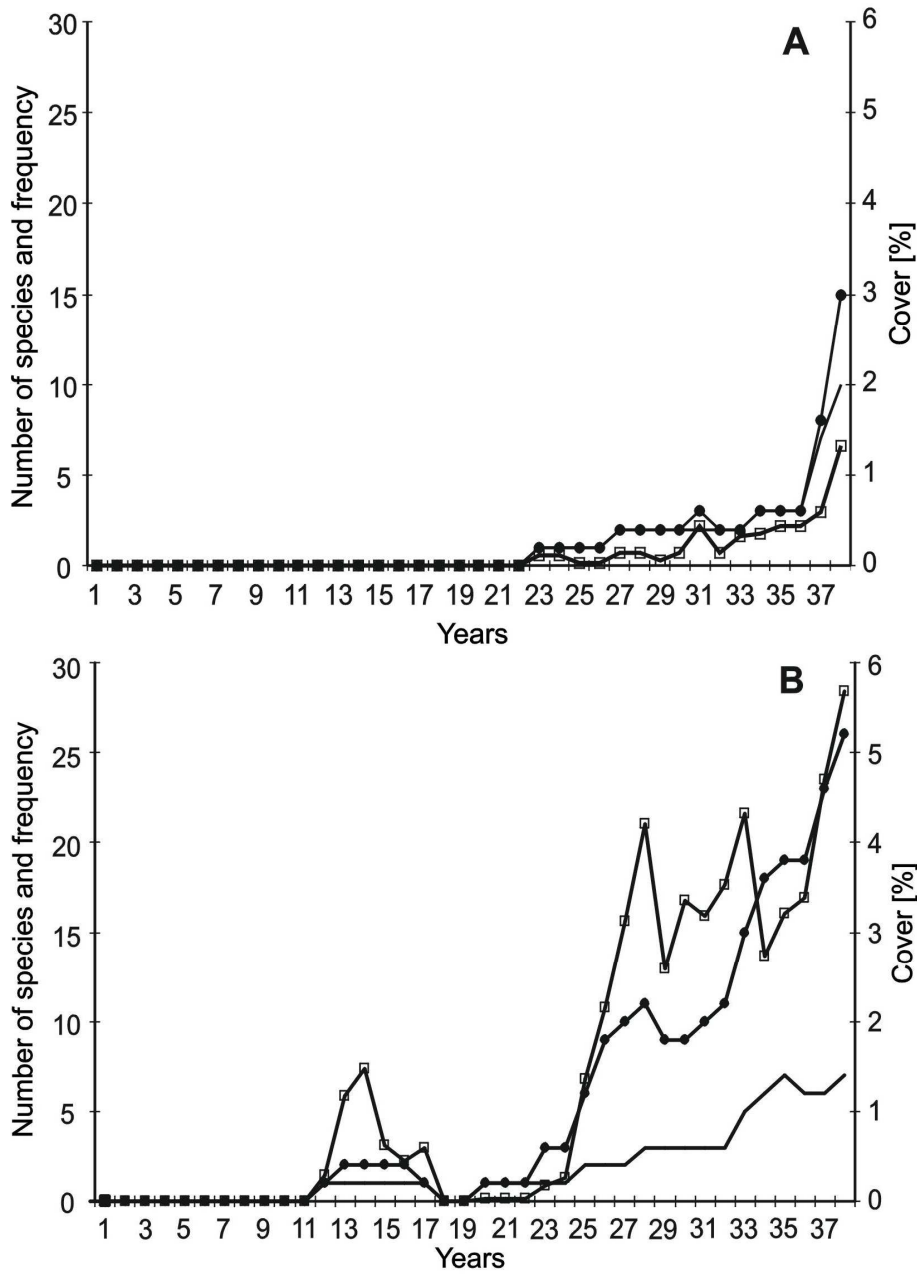


Fig. 4. Share of non-native taxa in the shrub layer in the course of secondary succession: number of species (line without marks —), frequency (line with black dots ●), cover (line with empty squares □). A - abandoned field, B - unmown meadow

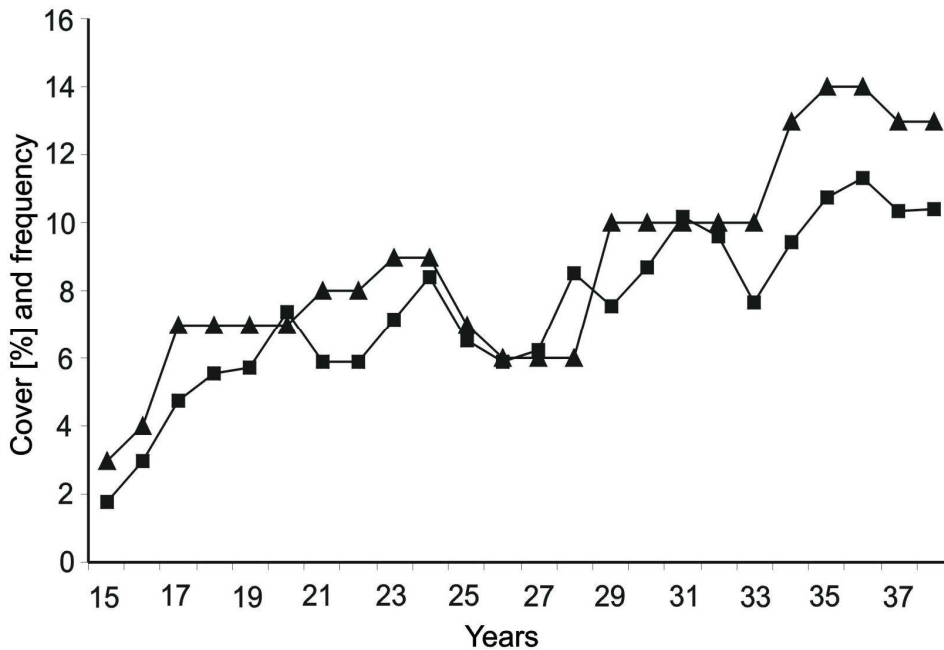


Fig. 5. Share of non-native taxa in the tree layer in the course of secondary succession on unmown meadow: frequency (line with black triangles ▲), cover (line with black squares ■)

Discussion

The study of secondary succession on the abandoned field and the unmown meadow conducted since 1974 in the Experimental Garden of Białowieża Geobotanical Station of Warsaw University confirmed the tendencies of encroachment of geographically alien taxa in this process in its different stages, simultaneously clearly showing the different behaviour of archaeophytes and kenophytes (especially woody ones) in the course of spontaneous succession.

The participation of a particular group of species measured by the number of species within a particular group present at a given time, the frequency of taxa belonging to a particular group at a given time, and the cover of taxa belonging to a particular group at a given time is different (compare Fig. 1, 2, 3), although there are some regularities. Taking into consideration all metaphytes growing on the abandoned field, their cover fluctuated, with a tendency to decrease (Fig. 3a), similar to other successional series (MEINERS *et al.* 2002; DÖLLE *et al.* 2008; BALCERKIEWICZ & PAWLAK 2011). On the unmown meadow the total number of anthropophytes was lower, particularly in first years of observation, the minimal number of anthropophytes was lower, and the subsequent rise in the number of anthropophytes was slower and more gradual (Fig. 1). The frequency (Fig. 2) and cover (Fig. 3) of anthropophytes in the ground layer was and still is lower on

the unmown meadow. This is a result not only of the higher number, frequency and cover of archaeophytes on the freshly abandoned field, but also an effect of more difficult germination conditions for trees and shrubs in compact grassy sod rather than in the loose weedy vegetation on the abandoned field (DUPRÉ & DIEKMANN 2001; KAHMEN & POSHLOD 2004). On the other hand, despite the higher number of woody kenophytes reaching the shrub layer on the abandoned field, their cover is still only about 1%, whereas on the unmown meadow it is 5%. It is the unmown meadow where *Malus domestica* and *Tilia platyphyllos* reached the tree layer, and are flowering and fruiting. This could be both a stochastic effect as well as difference in growth conditions (higher soil humidity due to the closeness of the irrigated culture plot to sector E – a crucial factor in dry periods). Unfortunately, one of the most important differences between our plots is the distance from the border of Palace Park, the most significant source of seed fall: sector E (former meadow) is located 40-65 m, and sector C (former field) - 115-140 m from the above-mentioned border (ADAMOWSKI & KNOPIK 1996), which makes any qualitative comparison of the influence of environmental conditions on the number and development of non-native taxa impossible.

Considered separately archaeophytes and kenophytes show different dynamical patterns in the course of succession. Similar to other studies (FALIŃSKI 1986; OSBORNOVÁ et al. 1990; DEBUSSCHE et al. 1991; DUPRÉ & DIEKMANN 2001; DÖLLE et al. 2008; BALCERKIEWICZ & PAWLAK 2011), the majority of archaeophytes, which are short-living species, quickly disappeared (Fig. 1). A striking exception is the behaviour of three vetches (*Vicia angustifolia*, *V. hirsuta*, *V. tetrasperma*) on the abandoned field, which reached maximum cover as late as seventh year of observation and tenth and eleventh years of observation (Fig. 3a) and were still present with high frequency until recently. However, in the last years we often found very small vetch specimens, without any flowers or fruits, so it is impossible to identify them at species level under field conditions – a clear symptom of their decline.

The presence of so many archaeophytes, which are typical elements of agrophytocoenoses, on the meadow plot (Fig. 1b) at the beginning of our study can be an effect of the recent change in land use from arable field to meadow. This hypothesis is also supported by very uneven species composition in different basal plots in first year of observation and high cover of *Elymus repens* (L.) Gould in the same time. The occurrence of obligatory weeds of arable fields could be, however, also an effect of sod disturbance when the experimental plots were established and fenced (ADAMOWSKI & BOMANOWSKA 2011b). It is worth mentioning that the cover value of archaeophytes on the meadow plot was almost six times lower than on the field plot at the beginning of our study (Fig. 3). The return of any archaeophyte in further stages of secondary succession seems to be unlikely without catastrophic phenomena like heavy windfall, gradation of insects or wildfire.

Amongst kenophytes herbaceous species behaved similarly to archaeophytes on the abandoned field (Fig. 1a, 2a, 3a). Up to now non-native shade-tolerant herbs, acting as *Alliaria petiolata* (M. Bieb.) Cavara & Grande in North America

(MEINERS et al. 2002), are absent in local flora. The last herbaceous kenophyte disappeared on the abandoned field in 26-th year of observation. On the unmown meadow this subgroup never played a significant role (Fig. 1b, 2b, 3b). These findings are in opposition to our previous studies conducted on the same physiographical area (the "open" Białowieża Clearing; ADAMOWSKI & BOMANOWSKA 2008). However, herbaceous kenophytes (*Conyza canadensis*, *Erigeron* sp., *Solidago gigantea*) were widespread in the rather open, grassy areas in Białowieża Clearing, whereas our successional plots have taken on a forest character recently. The encroachment of taxa like *Conyza canadensis*, *Impatiens parviflora* D.C., *Quercus rubra* L. and *Solidago* sp. into the shaping of vegetation on abandoned agricultural land has been confirmed in numerous studies in Poland (WĘGRZYNEK et al. 2005; STOSIK & KORCZYŃSKI 2007; BALCERKIEWICZ & PAWLAK 2011) and other countries (OSBORNOVÁ et al. 1990; DÖLLE et al. 2008).

On the other hand, since circa 18-th year of observation on both plots, the number of species, frequency and cover value of woody kenophytes occurring in the ground layer has been rising (Fig. 1, 2, 3). This phenomenon coincides with the development of the treestand, composed of pioneer species (*Betula pendula* Roth, *Populus tremula* L., *Salix caprea* L.), shading and outcompeting species typical for arable fields, fallows and grasslands, dominating in earlier phases of succession, as well as giving roosting places for birds (ADAMOWSKI & KNOPIK 1996; ADAMOWSKI & BOMANOWSKA 2011a). Recently 10 of these taxa reached the shrub layer on the abandoned field and seven on the unmown meadow (Fig. 4). It seems that woody species like *Malus domestica* and *Tilia platyphyllos* have the highest chance of permanent naturalization on our plots. Both these species are present in all layers of developing communities, and are flowering and fruiting. *Malus domestica* is one of the most common non-native woody taxa in the whole of Białowieża Forest; *Tilia platyphyllos* is much more confined, although it is regenerating freely in nearby Palace Park (ADAMOWSKI et al. 2002; W. ADAMOWSKI, pers. obs.). On the other hand, light-loving shrubby species (*Rosa* sp., *Crataegus* sp., *Cotoneaster lucidus* Schlttdl.), despite high frequency, grow very slowly and suffer high mortality. These taxa most probably disappear or diminish their share in ground layer vegetation in the course of the development of the mature treestand, composed of *Acer platanoides* L., *Carpinus betulus* L. and *Tilia cordata* Mill. In other studies (MEINERS et al. 2002; SCHMIDT et al. 2009) canopy closure appears to prevent invasions of open-adapted alien species.

The richness of woody alien flora on our successional plots is connected with the fact that the experimental plots are close to gardens and a park (ADAMOWSKI & KNOPIK 1996; ADAMOWSKI & BOMANOWSKA 2011a). Even in the same physiographical object (Białowieża Clearing) PABJANEK (2003) found only singular alien trees and shrubs in brushwoods lying more than 1000 m from the main settlement. Also in the study by BALCERKIEWICZ and PAWLAK (2011), despite rich cultivated and naturalized woody flora known from Wielkopolski

National Park (PURCEL 2009) only *Quercus rubra* reached the forest clearing which became the study area.

Considering woody kenophytes, two more phenomena are worth mentioning: *Quercus rubra* and *Acer negundo*, taxa well known as invasive species (DRESSEL & JÄGER 2002; WEBER 2003) are still rare on our plots despite abundant and regenerating populations in nearby Palace Park. Another is the prevalence of *Rosaceae* members in this group (15 out of 24 taxa). *Acer negundo* prefers more disturbed habitats (MĘDRZYCKI 2002); in the case of *Quercus rubra* this low presence could be a stochastic phenomenon, as juvenile plants of this species were seen at much longer distances from the source (ADAMOWSKI et al. 2002). The prevalence of *Rosaceae* amongst woody kenophytes is most probably an effect of a common biological feature (ornithochory), as many of them produce small, fleshy fruits, eaten by birds. *Crataegus* sp. and *Padus serotina*, both ornithochores, are amongst the five most frequently observed woody kenophytes in recent years (see Results).

The quick disappearance of archaeophytes (including only herbaceous plants, often annual or short living) and herbaceous kenophytes in the course of secondary succession, and the increasing diversity of non-native woody taxa coming from the nearby park and gardens are reasons for the absolute domination of these latter in the non-native flora of the study plots after time as short as 1/10 of the period necessary for the regeneration of *Tilio-Carpinetum* phytocoenosis (15-17 from 18-20 taxa on the abandoned field recently; Fig. 6).

The different behaviour of archaeophytes (decline) and kenophytes (more or less spread) is, at least partially, the result of the prevalence of different life forms in these groups (all archaeophytes are herbaceous, often short living, whereas 26 of 34 kenophytes are woody, this way easily overgrowing and outcompeting archaeophytes). Moreover, the majority of archaeophytes came from the Mediterranean region and south-west Asia, growing naturally in various open habitats (halophilous vegetation, coastal dunes, xerothermic grasslands, etc.; ZAJĄC 1979). Woody kenophytes came at least partially from the temperate forests of Europe, Asia and North America, and are apparently more shade tolerant – a clear advantage over light loving archaeophytes under the closing canopy of returning forest (compare MEINERS et al. 2002; DÖLLE et al. 2008).

Like other studies that have examined the role of non-native species in the course of secondary succession (MEINERS et al. 2002; MEINERS 2007; DÖLLE et al. 2008; SCHMIDT et al. 2009; TOGNETTI et al. 2010; BALCERKIEWICZ & PAWLAK 2011) our study confirmed that biological features, e.g. life form and life strategy, decide what role taxon is given in the succession process, and that the geographical origin of the species is of minor importance.

Up to now, geographically alien taxa, although present in all phases and stages of secondary succession, do not seem to have a negative influence on the richness and species diversity of the investigated plots (Fig. 7, 8). Non-native plants were unable to outcompete natives, as in the successional series investigated by MEINERS et al. (2001), YURKONIS & MEINERS (2004), TOGNETTI et al. (2010). This phenomenon is connected with high propagule pressure of native

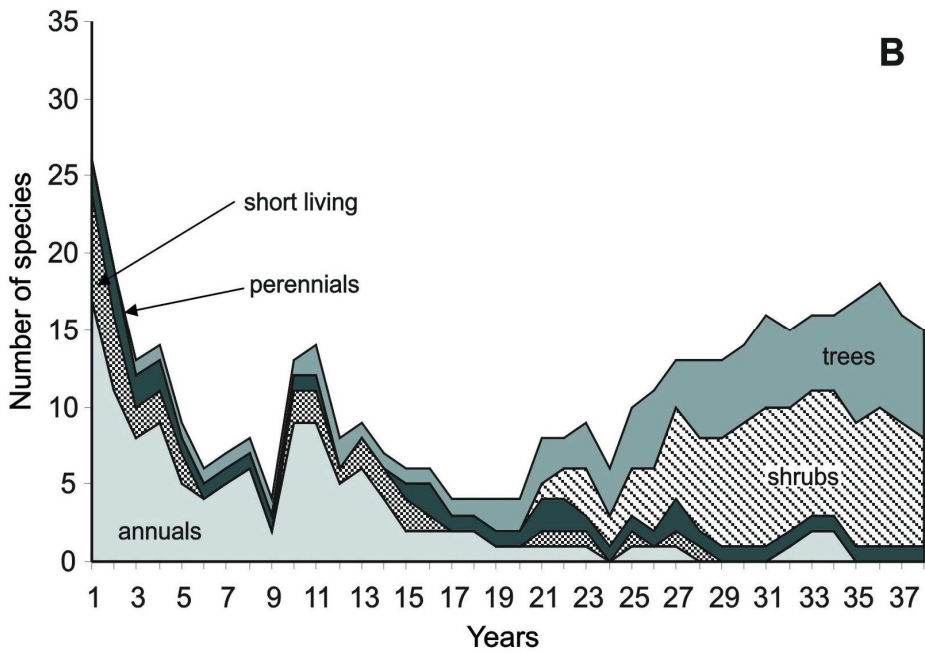
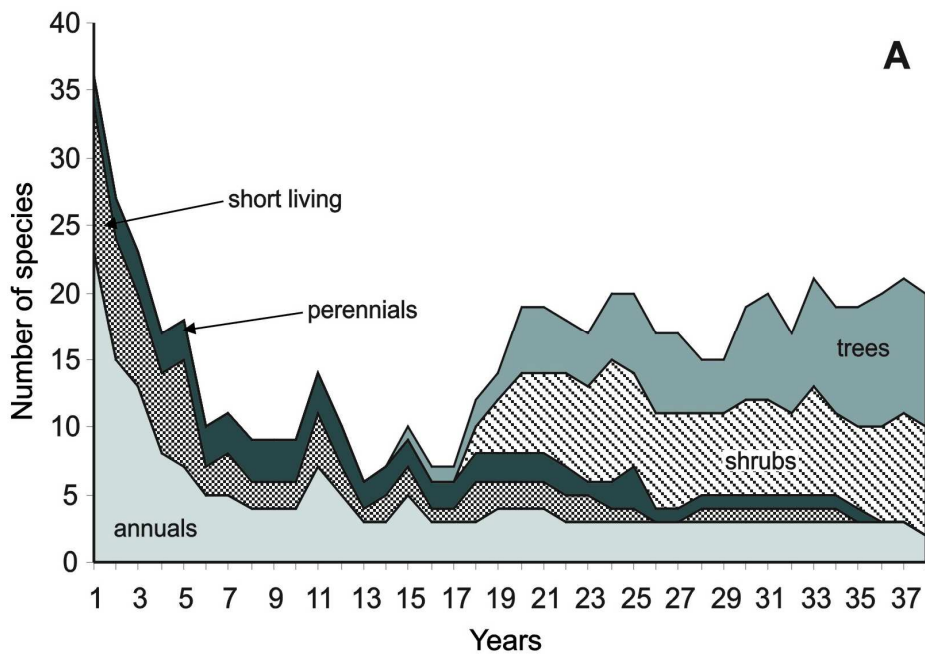


Fig. 6. Share of life forms of non-native taxa in the ground layer in the course of secondary succession. A - abandoned field, B - unmown meadow

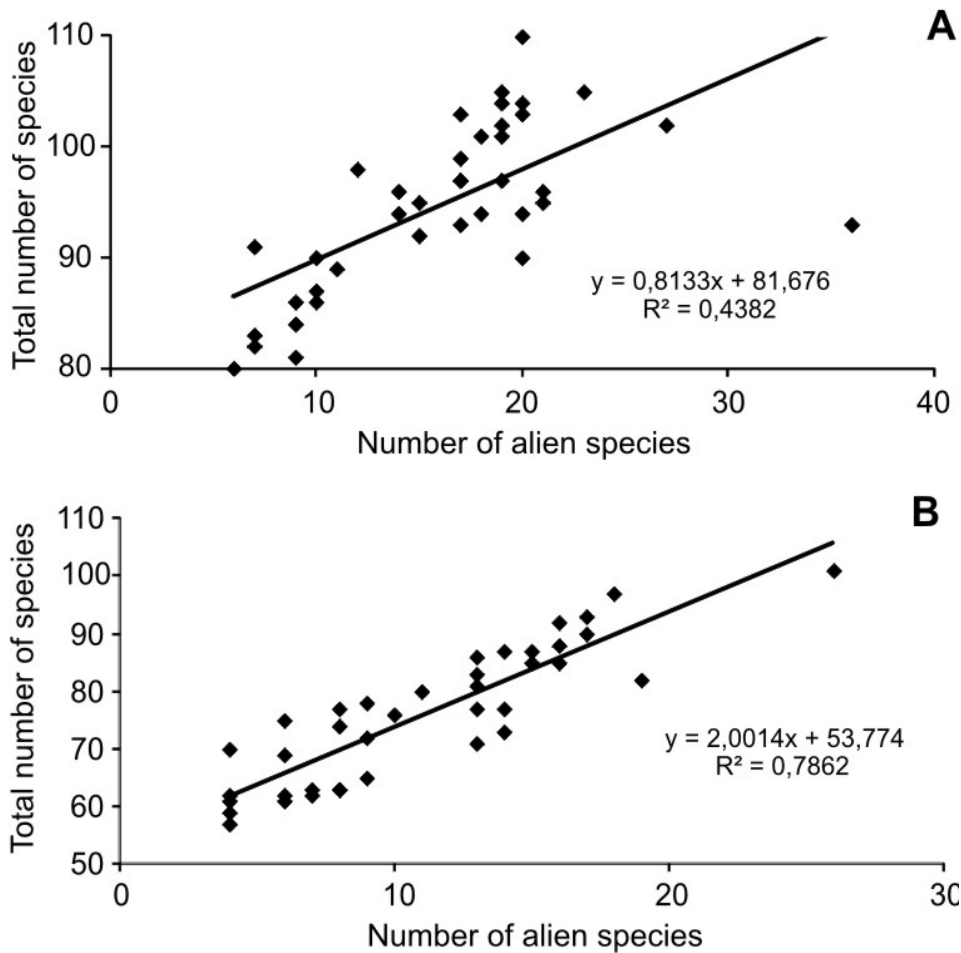


Fig. 7. Relation between number of non-native taxa and total number of taxa in the course of secondary succession. A - abandoned field, B - unmown meadow

forest species, like *Acer platanoides*, *Carpinus betulus* and *Tilia cordata*, also present in nearby Palace Park, as well as the good preservation state of the surrounding forest communities of Białowieża Forest (FALIŃSKI 1986; OKOŁÓW et al. 2009).

We predict that in the near future the last archaeophytes (*Vicia angustifolia*, *V. hirsuta* and *V. tetrasperma*), which are also the last herbaceous anthropophytes on our plots, will disappear from the abandoned field; most probably the same will be the fate of the lone herbaceous kenophyte on the unmown meadow, *Rumex confertus*. The encroachment of new herbaceous kenophytes (e.g. *Erigeron* sp., *Solidago* sp.) on both plots seems to be unlikely without catastrophic disturbance. We presume, however, at least a temporary rise in the

share of non-native woody taxa in ground layer vegetation. Prediction of the future share of kenophytes in the shrub layer and tree layer is even more difficult, almost impossible, on such small plots (we use data from 170 m²), where the death of one mature individual of almost any woody species will be visible in our data and will have further consequences for the course of the investigated process. A good illustration of these difficulties is the rather chaotic changes in the relative share of non-native taxa in the shrub layer and tree layer on the unmown meadow up to the present time (Fig. 9). However, at least *Malus domestica* and *Tilia platyphyllos* could become permanent components of the forest communities developing on our plots.

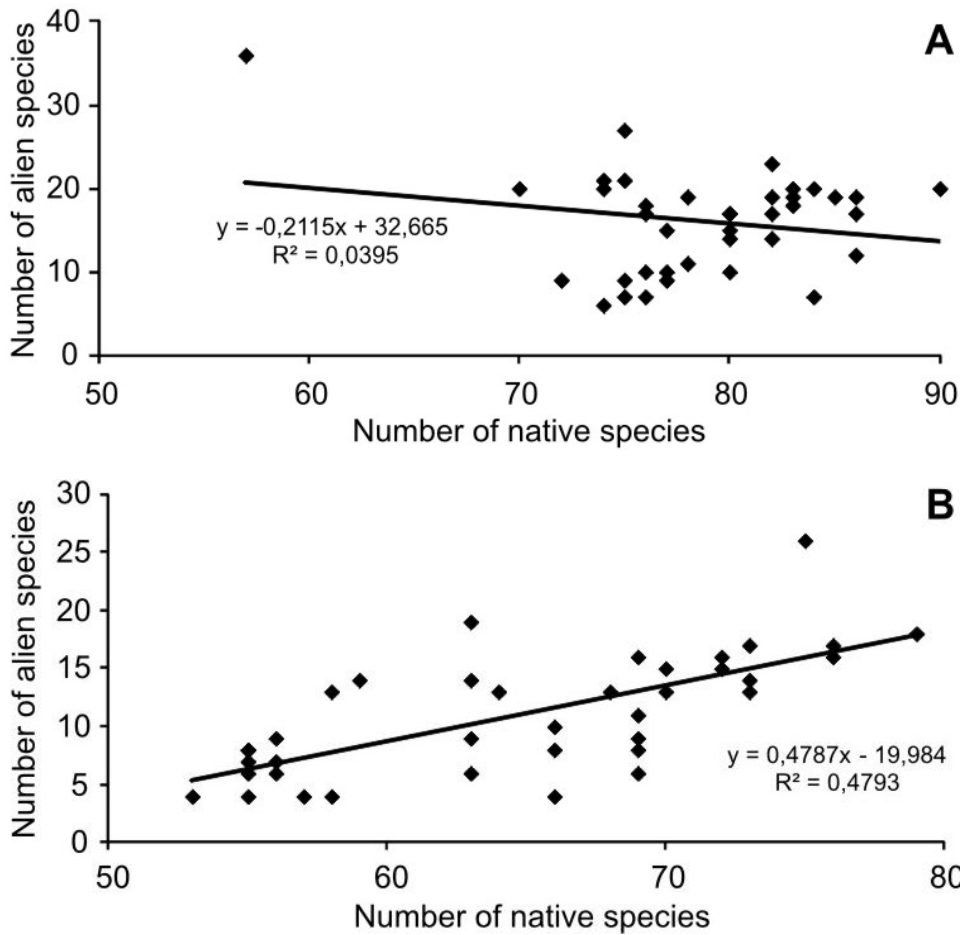


Fig. 8. Relation between number of native and non-native taxa in the course of secondary succession. A - abandoned field, B - unmown meadow

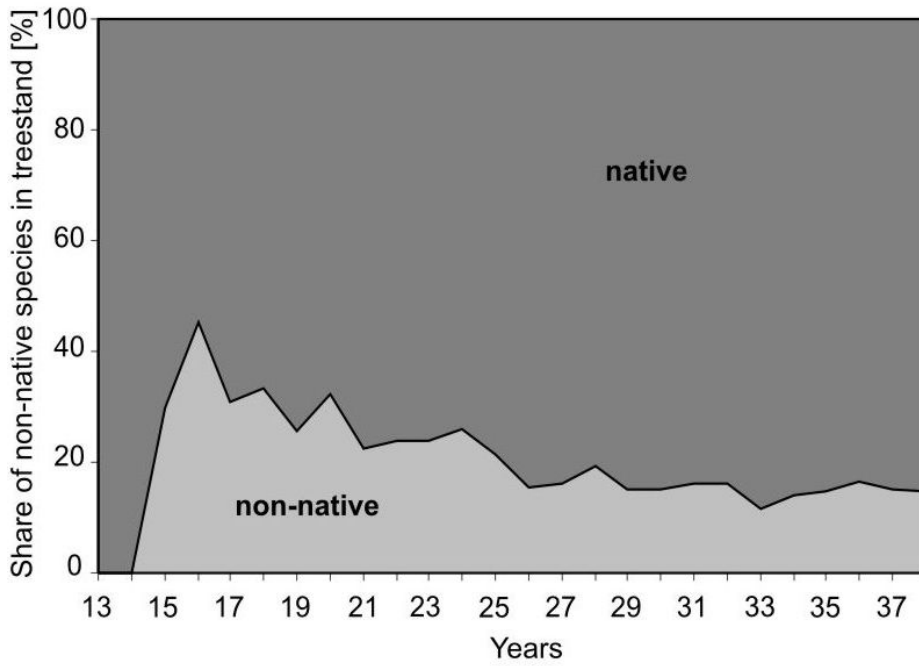
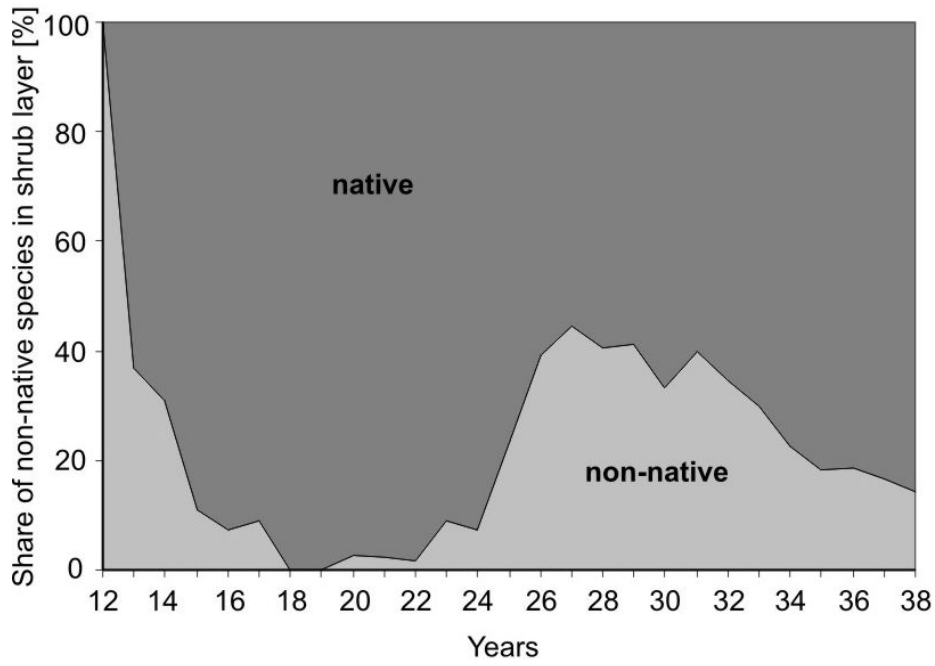


Fig. 9. Relative cover of non-native taxa in the course of secondary succession on unmown meadow. A – shrub layer, B - tree layer

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References

- ADAMOWSKI W. & BOMANOWSKA A. (2007): Udział drzew i krzewów obcego pochodzenia w procesie zasiedlania gruntów porolnych w rejonie Puszczy Białowieskiej (Occurrence of alien woody taxa in the colonization process of abandoned farmlands in the Białowieża Forest region). – *Acta Botanica Warmiae et Masuriae* 4: 309-320. (in Polish).
- ADAMOWSKI W. & BOMANOWSKA A. (2008): Zmiany użytkowania gruntów na obrzeżach cennych obiektów przyrodniczych a wkraczanie nierodzimych gatunków roślin (Changes of land use on the borders of valuable natural areas and expansion of alien plant species). – *Przegl. Przyr.* 19,3/4: 3-17. (in Polish).
- ADAMOWSKI W. & BOMANOWSKA A. (2011a): Forest return on an abandoned field – secondary succession under monitored conditions. – *Folia Biol. Oecol.* 7: 49–73.
- ADAMOWSKI W. & BOMANOWSKA A. (2011b): Udział traw w sukcesji wtórnej na niekoszonej łące łąkowej w Puszczy Białowieskiej (Share of grasses in secondary succession on unmown meadow in Białowieża Forest). – *Fragm. Flor. Geobot. Polonica* 18(2): 375-385. (in Polish).
- ADAMOWSKI W., DVORAK L. & RAMANJUK I. (2002): Atlas of alien woody species of the Białowieża Primateval Forest. – *Phytocoenosis (N.S.)* 14. Suppl. *Cartogr. Geobot.* 14: 1-303.
- ADAMOWSKI W., MĘDRZYCKI P. & ŁUCZAJ Ł. (1998): The penetration of alien woody species into the plant communities of the Białowieża Forest: the role of biological properties and human activities. – *Phytocoenosis (N.S.)* 10. Suppl. *Cartogr. Geobot.* 9: 211-228.
- ADAMOWSKI W. & KNOPIK A. (1996): Ornithochorous species penetration onto abandoned farmland during secondary succession. – *Phytocoenosis* 8 (N.S.) *Sem. Geobot.* 4: 97-110.
- BALCERKIEWICZ S. & PAWLAK G. (2011): Antropofity na tle dynamiki roślinności – studium na podstawie długoterminowego eksperymentu na powierzchni stałej (Anthropophytes in vegetation dynamics: a long-term study on a permanent plot). – *Acta Bot. Siles.* 6: 63-80. (in Polish).
- BANASIAK S. E. & MEINERS S. J. (2009): Long term dynamics of *Rosa multiflora* in a successional system. – *Biol. Invasions* 11: 215–224.
- BARABASZ-KRASNY B. (2002): Sukcesja roślinności na łąkach, pastwiskach i nieużytkach porolnych Pogórza Przemyskiego (The succession of vegetation on the meadows, pastures and barren agricultural areas in the Przemyśl Foothills (south-eastern Poland)). – *Fragm. Flor. Geobot. Polonica Suppl.* 4: 3-81. (in Polish).
- BOMANOWSKA A. & ADAMOWSKI W. (2007): Grasses (Poaceae) in secondary succession of oak-hornbeam series in Białowieża Forest. – In: FREY L. (ed.): *Biological issues in grasses*, p. 131-143. – W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.
- BOMANOWSKA A. & ADAMOWSKI W. (2009): The role of woody species in the secondary succession under monitored conditions (Białowieża Forest, NE Poland). – In: IVANOVA D. (ed.): *Plant, fungal and habitat diversity investigation and conservation. Proceedings of IV Balkan Botanical Congress, Sofia, 20-26 June 2006*, p. 291-295. – Institute of Botany, Bulgarian Academy of Sciences, Sofia.

- BOMANOWSKA A. & KIEDRZYŃSKI M. (2011): Changing land use in recent decades and its impact on plant cover in agricultural and forest landscapes in Poland. – *Folia Biol. Oecol* 7: 5-26.
- BRAUN-BLANQUET J. (1964): *Pflanzensoziologie. Grundzüge der Vegetationskunde*. 3., p. 865. – Springer-Verlag, Wien-New York.
- DEBUSSCHE M., ESCARRÉ J., LEPART J., HOUSSARD C. & LAVOREL S. (1996): Changes in mediterranean plant succession: old-fields revisited. – *J. Veg. Sci.* 7: 519-526.
- DÖLLE M., BERNHARDT-RÖMERMANN M., PARTH A. & SCHMIDT W. (2008): Changes in life history trait composition during undisturbed old-field succession. – *Flora* 203: 508-522.
- DRESSEL R. & JÄGER E. J. (2002): Beiträge zur Biologie der Gefäßpflanzen des herzynischen Raumes. 5. *Quercus rubra* L. (Roteiche): Lebengeschichte und agriophytische Ausbreitung im Nationalpark Sächsische Schweiz. – *Hercynia N. F.* 35: 37-64.
- DUPRÉ C. & DIEKMANN M. (2001): Differences in species richness and life-history traits between grazed and abandoned grasslands in southern Sweden. – *Ecography* 24: 275-286.
- FALIŃSKA K. (2003): Alternative pathways of succession: species turnover patterns in meadows abandoned for 30 years. – *Phytocoenosis* 15 (N.S.) *Archiv. Geobot.* 10: 1-104.
- FALIŃSKI J. B. (1986): Vegetation dynamics in temperate lowland primeval forests. Ecological studies in Białowieża Forest. *Geobotany* 8, p. 1-537. – Dr W. Junk Publishers, Dordrecht/Boston/Lancaster.
- FALIŃSKI J. B. (1988): Succession, regeneration and fluctuation in the Białowieża Forest (NE Poland). – *Vegetatio* 77: 115-128.
- FALIŃSKI J. B. (1998): Invasive alien plants and vegetation dynamics. – In: STARFINGER U., EDWARDS K., KOWARIK I., WILLIAMSON M. (eds): *Plant invasions. Ecological consequences and human responses*, p. 3-21. – Backhuys, Leiden.
- FALIŃSKI J. B. (2002): Białowieża Geobotanical Station. Long-term studies. Data basis on the vegetation and environment (1952-2002). – *Phytocoenosis* 14 (N.S.) *Suppl. Bibl. Geobot.* 14: 1-200.
- FIKE J. & NIERING W. A. (1999): Four decades of old field vegetation development and the role of *Celastrus orbiculatus* in the northeastern United States. – *J. Veg. Sci.* 10: 483-492.
- GRINN-GOFRON A. (2007): Zbiorowiska zastępcze w monokulturach sosnowych na gruntach porolnych (The forest secondary communities in the pine monocultures on abandoned farmlands). – *Acta Botanica Warmiae et Masuriae* 4: 269-282. (in Polish).
- JACKOWIAK B. (1990): Antropogeniczne przemiany flory roślin naczyniowych Poznania (Anthropogenic changes of the flora of vascular plants of Poznań). *Wyd. Naukowe Univ. Adama Mickiewicza, ser. Biol.* 42: 1-208. (in Polish).
- KAHMEN S. & POSHLOD P. (2004): Plant functional trait responses to grassland succession over 25 years. – *J. Veg. Sci.* 15: 21-32.
- KORNAŚ J. (1977): Analiza flor synantropijnych (Analysis of synanthropic floras). – *Wiad. Bot.* 21: 85-91. (in Polish).
- LONDO G. (1976): The decimal scale for relevés of permanent quadrats. – *Vegetatio* 33: 61-64.
- ŁASKA G. (1997): Kształtowanie się leśnych zbiorowisk zastępczych na terenach użytkowanych rolniczo (The formation of the secondary forest communities on the areas used for agricultural purposes). – *Przegl. Przyr.* 8, 1/2: 77-86. (in Polish).

- MĘDRZYCKI P. (2002): Inwazja amerykańskiego klonu *Acer negundo* L. a użytkowanie ziemi w Puszczy Białowieskiej (Invasion of American *Acer negundo* L. and land use in Białowieża Forest), p. 96 + Aneks A + Aneks B. – Praca doktorska, Uniwersytet Warszawski, Warszawa – Białowieża. (in Polish).
- MEINERS S. J. (2007): Native and exotic plant species exhibit similar population dynamics during succession. – *Ecology* 88, 5: 1098-1104.
- MEINERS S. J., PICKETT S. T. A. & CADENASSO M. L. (2001): Effects of plant invasions on the species richness of abandoned agricultural land. – *Ecography* 24: 633–644.
- MEINERS S. J., PICKETT S. T. A. & CADENASSO M. L. (2002): Exotic plant invasions over 40 years of old field successions: community patterns and associations. – *Ecography* 25: 215-223.
- MIREK Z. (1981): Problemy klasyfikacji roślin synantropijnych (Problems of classification of synanthropic plants). – *Wiad. Bot.* 25: 45-54. (in Polish).
- MIREK Z., PIĘKOŚ-MIRKOWA H., ZAJĄC A. & ZAJĄC M. (2002): Flowering plants and pteridophytes of Poland – a checklist. – In: MIREK Z. (eds): Biodiversity of Poland 1, p. 442. – W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.
- OKOŁÓW C., KARAŚ M., BOŁBOT A. (2009): Białowiecki Park Narodowy. Poznać - Zrozumieć – Zachować (Białowieża National Park. Know it – Understand it – Protect it), p. 240. Białowiecki Park Narodowy, Białowieża.
- OSBORNOVÁ J., KOVÁROVÁ M., LEPS J. & PRACH K. (1990): Succession in abandoned fields. Studies in Central Bohemia, Czechoslovakia, p. 168. – Kluwer Academic Publishers, Dordrecht.
- PABJANEK P. (2003): Kształtowanie się zapustów leśnych w warunkach puszczańskiej polany osadniczej (The establishment of brushwoods in conditions of forest settlement clearing), p. 65. – PhD thesis, Uniwersytet Warszawski, Warszawa – Białowieża. (in Polish).
- PURCEL A. (2009): Obce gatunki drzew i krzewów w Wielkopolskim Parku Narodowym - ich występowanie i rola w biocenozach Parku (Alien trees and shrubs in Wielkopolski National Park - their occurrence and role in Park's biocoenoses). – *Morena* 14: 35-191.
- REJMÁNEK M. (1989): Invasibility of plant communities. – In: Drake J. A. et al. (eds.): Biological invasions: a global perspective, p. 369-388. – John Wiley & Sons, Chichester, New York, Brisbane, Toronto, Singapore.
- REJMÁNEK M. (1999): Invasive plant species and invulnerable ecosystems. – In: SANDLUND O. T., SCHEI P. J., VIKEN Å. (eds): Invasive species and biodiversity management, p. 79-102. – Kluwer Academic Publishers, Dordrecht/Boston/London.
- SCHMIDT W., DÖLLE M., BERNHARDT-RÖMERMANN M., PARTH A. (2009): Neophyten in der Ackerbrachen-Sukzession-Ergebnisse eines Dauerflächen-Versuchs. – *Tuexenia* 29: 236-260.
- SOKOŁOWSKI A.W. (1995): Flora roślin naczyniowych Puszczy Białowieskiej (The flora of vascular plants in the Białowieża Forest), p. 1-275. – Białowiecki Park Narodowy, Białowieża.
- STOSIK T. & KORCZYŃSKI M. (2007): Zbiorowiska roślinne porzuconych pól uprawnych w Borach Tucholskich (Plant communities of abandoned fields in Bory Tucholskie). – *Acta Botanica Warmiae et Masuriae* 4: 123-134. (in Polish).
- TOGNETTI P. M., CHANETON E. J., OMACINI M., TREBINO H. J. & LEÓN R. J. C. (2010): Exotic vs. native plant dominance over 20 years of old-field succession on set-aside farmland in Argentina. – *Biological Conservation* 143: 2494-2503.
- TOKARSKA-GUZIŁ B. (2005): The Establishment and Spread of Alien Plant Species (Kenophytes) in the Flora of Poland, p. 192. – Wyd. Uniw. Śląskiego, Katowice.

- WEBER E. (2003): Invasive plant species of the world, p. 548. – CABI Publishing, Wallingford.
- WĘGRZYNEK B., URBISZ A. & NOWAK T. (2005): Participation of *Solidago canadensis* L. and *S. gigantea* Aiton in abandoned field communities in the Silesian Upland (Poland). – *Thaiszia* 15, Suppl. 1: 267-275.
- YURKONIS K. A. & MEINERS S. J. (2004): Invasion impacts local species turnover in a successional system. – *Ecology Letters* 7: 764–769.
- ZAJĄC A. (1979): Pochodzenie archeofitów występujących w Polsce (The origin of the archaeophytes occurring in Poland). – *Rozpr. Habil. Uniw. Jagiell.* 29: 1-213. (in Polish).
- ZAJĄC A. & ZAJĄC M. (2011): Methodical problems in distinguishing the group of archaeophytes. – *Acta Bot. Siles.* 6: 55-62.

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