Ann. Bot. Fennici 50: 1–12 ISSN 0003-3847 (print) ISSN 1797-2442 (online)
Helsinki 12 April 2013
© Finnish Zoological and Botanical Publishing Board 2013

The white stork as an engineering species and seed dispersal vector when nesting in Poland

Joanna Czarnecka[1,*] & Ignacy Kitowski[2]

[1)] *Ecology Department, Institute of Biology and Biochemistry, Maria Curie-Skłodowska University, Akademicka 19, PL-20-033 Lublin, Poland (*corresponding author's e-mail address: a_czarnecki@wp.pl)*
[2)] *State School of Higher Education in Chełm, Pocztowa 54, PL-20-100 Chełm, Poland*

Received 5 July 2012, final version received 20 Dec. 2012, accepted 28 Dec. 2012

Czarnecka, J. & Kitowski, I. 2013: The white stork as an engineering species and seed dispersal vector when nesting in Poland. — *Ann. Bot. Fennici* 50: 1–12.

The white stork can affect plant population and community dynamics and structure in an agricultural landscape. It is a vector transporting large numbers of seeds along with nest material, and it is an ecosystem engineer which builds nests that function as specific habitats for plants. The following questions were asked: (i) What is the structure of the seed pool in the nest material? (ii) Can nests be treated as a habitat enabling plants to complete their life cycle? (iii) What is the probability that seeds produced in the nests reach suitable habitats in the nests' closest vicinity? Seed pools of ten white-stork nests were analysed using the seedling germination method. The average number of seedlings detected in the nest material was 9937 per one nest (870 per 10 000 g of dry weight); they belonged to 97 taxa. Majority of the species present in the nests created persistent seed banks (62.5%); 62.2% of the seedlings represented annual species. Significantly higher percentage of weeds and significantly lower of woodland and peat-bog species in the nests as compared with the respective percentages of these species groups in the regional pool, indicated arable fields and ruderal sites as the main sources of seeds as well as the nest material. Since ruderal species and weeds dominated in the seed pool found in the nests, and such habitat types were most common in the vicinity of the nests, the probability that seeds produced in the nests would disperse into a suitable habitat was high.

Introduction

Complexity of interactions between organisms and abiotic factors has been widely recognised. One organism can affect another via a number of different ways, e.g., by being a vector and/or an ecosystem engineer (Wright & Jones 2006). Although the concept of ecosystem engineering is quite recent, researchers quickly realized its importance for understanding ecosystem functioning and for conservation efforts at population, community and ecosystem levels (Jones *et al*. 1994, Laland & Boogert 2010). Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species by causing physical changes in biotic and abiotic matter. They create, modify or maintain existing habitats. As a rule, activities of these organisms do not involve direct trophic interactions; they affect energy and matter flows in an ecosystem by creating or destroying living space, and thereby altering environments of other organisms. Positive ecological effects of engineers' activity are very common; they appear in all environments and cannot be ignored (Jones *et al*. 1994, 1997, Brown 1995, Wright & Jones 2006).

Animals building nests and burrows are good examples of engineering species. The primary function of nests is hazard mitigation but they also affect habitats in which they are built. Nests create a new range of habitat niches, which can be used by a variety of organisms (Hansell 1993). The impact of one particular ecological engineer depends upon the spatial and temporal scales of its action, but even ephemeral nests constructed by small passerines can be an example of the effect of ecosystem engineering (Jones *et al*. 1994).

The white stork (*Ciconia ciconia*) — a species connected with the agricultural landscape of central Europe — is a good example of an ecosystem engineer. The population of the white stork in Poland is estimated at about 52 000 breeding pairs, i.e., about 20% of the world population (Guziak & Jakubiec 2006, Tryjanowski *et al*. 2009). White storks build large and long-lasting nests (up to 2 m in height and 1.5 m in diameter, existing from several years to several decades), which are repaired and extended each year during the whole breeding season. Nest material (twigs, sticks, hay, straw, grass, soil and dung) is collected mainly from the ground in the vicinity of the nest. The transfer of material between nests is also possible. Sometimes one pair occupies more than one nest and these additional nests (called satellites) can serve as sources of nest material. Stealing of material from occupied nests also happens very often (Bocheński & Jerzak 2006, Indykiewicz 2006, Tryjanowski *et al*. 2009). One particular nest is usually occupied for four months a year (Indykiewicz 2006). About 10% of the nests are left unoccupied every year (data from The Biebrza valley, Nowakowski 2006); the continuous nest-occupancy index for lowland-located nests is about five years (Tryjanowski *et al*. 2005). Nests are located in the vicinity of human settlements (the white stork is a species typical to villages), and 60% of them are placed on electricity poles (Tryjanowski *et al*. 2009).

Long-lasting nests of this bird are habitats often used as nesting places by other birds, the most common co-occupants being the sparrow *Passer* spp., the starling *Sturnus vulgaris*, the grey wagtail *Motacilla alba*, and the kestrel *Falco tinnunculus*. Other vertebrates may also reside in nest: e.g. the Norway rat *Rattus norvegicus* and the striped field mouse *Apodemus agrarius* were found nesting there (Bocheński & Jerzak 2006, Indykiewicz 2006, Kosicki *et al*. 2007).

Although the biology and behaviour of the white stork is well known, we were not able to find any studies on the role of this species in plant population dynamics and seed dispersal. Our observations indicate the nests of the white stork as specific habitats where seed germination, seedling stabilization, blooming and producing a new pool of seeds very often take place. Our goal was to answer the following questions concerning consecutive stages of plant-life history: (i) What is the structure of the seed pool in the nest material? (ii) Can the nests be treated as a habitat enabling plants to complete their life cycle? (iii) What is the probability that seeds produced in nests reach suitable habitats in the nests' closest vicinity? The main hypothesis was that the white-stork nests can function as microhabitats if the conditions there meet specific plant requirements. Previous findings (Czarnecka *et al*. 2010) and knowledge of the white stork breeding behaviour led us to hypothesize that the nests can be a suitable habitat for annual species with persistent seed banks, adapted to open and nutrient-rich habitats and resistant to drying. Firstly, only persistent seeds can remain dormant until it is possible to germinate in a nest (only small fraction of seeds germinate after seed transfer into the nests, the majority of them remains alive in the nest material). Secondly, a short life span enables a species to close its life cycle in one vegetative season, or even in a shorter time after young storks abandon the nest, and to produce the next set of seeds. Biennials and perennials can also be able to complete their life cycle in nests but the probability of their success is lower.

Material and methods

Study area and methods of data collecting

In March 2007, nest material (lining) was collected from central parts of ten nests located on electricity poles in the villages in the vicinity of Chełm (central part of eastern Poland). Extensive farming is typical for the region (Chylarecki *et al*. 2006). The average area of arable fields, meadows and forest patches is small, with a relatively dense network of linear landscape elements like field roads, balks and hedgerows, as well as scattered housing. Approximately 20 dm^3 of the lining material (ca. 10% of all lining material gathered from the nest) was taken during the routine maintenance work on the power grid done before the arrival of birds. The studied nests were similar in size: 0.5 m high and 1.5 m in diameter. It was estimated that 80% of their volume was lining material and the remaining part were sticks and twigs, which stabilised and strengthened the nest structure. To study the seed pool of the nests, the seedling emergence method was applied (Thompson *et al*. 1997). The nest material (15 dm^3 for each nest) was put into plastic trays and kept moist in cold frames placed in an experimental garden for the duration of two subsequent vegetative seasons (March–November, lining was left in the garden during winter to let the seeds left to be stratified). All emerging seedlings were counted, identified and removed. The amount of seedlings per one nest and per 10 000 g (dry weight) of nest material was counted to facilitate comparisons and statistical analyses of the obtained data.

The remaining material was dried to assess the dry weight (d.w.) of 1 dm^3 of the substratum, and to analyse its physicochemical properties which was done in accredited laboratories according to ISO/IEC 17025:2005 (Forest Research Institute [Accreditation Certificate of Testing Laboratory AB740] and Regional Chemical-Agricultural Station in Lublin [DAP-PL-3413, Accredited testing laboratory by DAP Deutsches Akkreditierungssystem Prüfwesen GmbH]). All samples were treated as organic substratum and the following analytical methods were used: total nitrogen (N) was analysed with the macro analyser VarioMax CN (Elementar Analysensysteme GmbH), pH in 1 M KCl according to PN-ISO 10390:1997; P_2O_5 according to PN-R-04024:1997; K_2O according to PN-R-400024:1997; Mg according to PN-R-40024:1997; Zn according to PN-92/R-04016; Cu according to PN-92/R-04017; Mn according to PN-93/R-04019 and Fe according to PN-R-04021-1994. We compared the results of chemical analyses with border values for arable soils or mean values for Polish soils (IUNG 1990, Zawadzki 1999).

The surroundings of the nests were studied within a 100-m radius, because we assumed that seeds produced in the nests would mostly be locally dispersed. The chosen radius is often considered a border value distinguishing local and long-distance dispersal (Cain *et al*. 2000, Nathan *et al*. 2008). Five main habitat types were identified: arable fields, meadows, ruderal sites (e.g. field and road margins, backyards, small gardens and other disturbed areas), forests, and buildings. Their areas and percentages were estimated on aerial photographs with the help of the ArcMap10 programme.

Data analysis

The main sources for species life-history traits related to regeneration (dispersal mode, seed bank type) were Kleyer *et al*. (2008), Thompson *et al*. (1997) and Grime *et al*. (1996) (also Davies & Waite 1998, Drezner *et al*. 2001, Leck & Schuts 2005, Mathus *et al*. 2005, Palisar 2006, Koutecká & Lebš 2009). The term ‘persistent’ was used for both short- and long-term persistent seed-bank types (classification according to Bakker *et al*. 1996).

Life form of plants (annuals *vs*. perennials) is given according to Zarzycki *et al*. (2002). Species as ecological indicators and their grouping follows Zarzycki *et al*. (2002). Their groupings are similar to Ellenberg’s *et al*. (1991), but were developed exclusively for Polish flora, and are thus more accurate for the present study. We used three ecological factors of Zarzycki *et al*. (2002): (1) light value to indicate light requirements of plants (ranging from 1 to five, where 1 = full shade and 5 = full light); (2) soil trophic state (ranging between 1 and 5, where 1 = extremely poor and 5 = extremely fertile); and (3) soil moisture value (ranging between 1 and 6, where 1 = very dry soils, 5 = wet soils and 6 = aquatic habitats).

The seedling pool of the nests was compared with the expected species pool defined as the species present at a regional scale whose diaspores could have a chance to be incorporated into the nest material. The χ^2 likelihood ratio test (Łomnicki 2010) was used for that purpose. The regional species list was constructed using the data for the eastern part of the Lublin Upland (the western border was the Wieprz river) taken from Zając and Zając (2001). Considering behaviour of storks, aquatic plant species were excluded from the analysis as were also orchids, because their seeds cannot be detected with the seedling germination method. The list of species belonging to Poaceae, *Carex* and *Rubus* was narrowed down to species easily distinguishable in vegetative stage. Only fully identified species present in the seedling pool of the nests were included in the analysis.

When life-history traits and habitat requirements were analysed, only weeds, ruderal-meadow and grassland species were included in the expected species list.

Differences in species richness of different functional groups of plants present in the nests' seedling pool were analysed with Student‘s *t*-test and ANOVA. One nest was treated as a sample (n = 10). These analyses were used to find the pattern in the nest seeding pool and to check if habitat features in the nests meet the requirements of species which germinated there. Normality of the data was tested with the Shapiro-Wilk test, and equality of variances of analysed samples with Levene's test (Stanisz 1998). All calculations were performed using Statistica PL.

Results

Seedling pool of nests

The number of seedlings detected in the nest material of the studied nests varied between 5580 and 14 759 per one nest (mean = 9937, n = 10; Table 1). Majority of the seedlings (80%) germinated in the first study year. Recorded species belonged to 97 taxa. It was mostly possible to identify the species (85); however, in few cases, the order (10 orders) or the family only (two families, Fabaceae and Poaceae) were identified (Appendix 1). A group of species with high frequency (understood as the percentage of the nests that contained a given species) could be distinguished. *Chenopodium album* was the most abundant in almost all the nests. *Medicago lupulina* and *Poa annua* were present in the lining of all the nests. Frequencies of 12 other species exceeded 50%.

Three distinct ecological groups of species were distinguished in the nests: (1) weeds and ruderal species, which were the most abundant (mean number of species = 17.1, percentage in the total number of seedlings = 78%), (2) meadow species (6.2 and 17%, respectively), and (3) other taxa with significant percentage of woodland, peat-bog and rush species (2.4 and 5.3%, respectively; Table 2 and Appendix 1). Significantly higher percentage of weeds and significantly lower percentage of woodland and peat-bog species in nests, as compared with their percentages in the regional flora, identified

Table 1. Seedlings recorded in the studied nests (for more information *see* Appendix 1).

Character	Nest number										Mean
	1	2	3	4	5	6	7	8	9	10	
Number of seedlings											
per one nest	14759	10555	6937	7631	7693	12036	10725	9128	5580	14322	9937
per 10 000 g (d.w.)	1520	930	410	690	320	1770	750	970	450	930	870
Number of taxa recorded	32	16	21	31	33	37	38	23	24	31	28.6

arable fields and ruderal sites as the main sources of seeds and nest material (Table 2).

Majority of the species found in the nests created persistent seed banks (62.5% as compared with 34.1% in the regional species pool; Table 3). Their seedlings constituted on average 84% ($n = 10$) of the total seedling number in all the studied nests. It confirmed that the presence of long-living seeds increased the chance of germination in the nests. The proportion of annuals in the nest seed pool equalled their proportion in the regional flora (Table 3).

Habitat characteristics *versus* plant life-history traits

Physicochemical analysis of the properties of the substratum revealed that the habitat was acidic and nutrient-rich, with high or even very high contents of the most common macro- and microelements (Appendix 2). These microhabitat conditions seemed to be suitable for the vast majority of species found in the nest material. Percentage of rich-habitat species was significantly higher in the nests than in the regional flora (Table 4). Nests of the white stork could also be described as open habitats subject to drying. The seedling pool found in the nests was dominated by species adapted to such habitats, and their proportion in the nests reflected the structure of the regional flora (Table 4).

Nest surroundings, a chance for dispersal into suitable habitats

The mean percentages of ruderal habitats and arable fields in the vicinity of the nests were 53% and 18%, respectively, and their sum (71%) was significantly higher than the abundances of other habitat types (meadows 15%, buildings 11%, forests 3%) (ANOVA: $F_{2,27} = 58.2$, $p < 0.001$). Since ruderal species and weeds dominated in the seed pool found in the nests, the probability that seeds produced in the nests would disperse into a suitable habitat was high.

The most distinct feature of the seedling pool of the nests was high percentage of barochorous (seeds dispersed by gravity) species (67%, mean number of species per nest = 15.7, $n = 10$) as compared with that of species with other dispersal modes (33%, mean number of species per nest = 10.6, $n = 10$) (t-test: $t_9 = 2.60$, $p < 0.05$). The most common dispersal adaptation among the species found in the nests was exozoochory (23% on average); percentages of species with other dispersal adaptation did not exceed

Table 2. Percentages (numbers in parentheses) of species belonging to different ecological groups found in the regional flora and in the white-stork nests. Proportion of ecological groups in the regional species pool was treated as the expected value in the χ^2-test (df = 2).

Species pool	Ecological groups			χ^2 statistics
	Weed and ruderal	Meadow	Others*	
Regional flora	28.9 (229)	35.0 (278)	36.1 (286)	$\chi^2 = 34.608$, $p < 0.001$
Nests	56.0 (47)	30.9 (26)	13.1 (11)	

* mostly woodland, peat-bog and rush species.

Table 3. Percentages (numbers in parentheses) of species with different life-history traits found in the regional flora and in the white-stork nests. Proportion of species in the regional pool was treated as the expected value in the χ^2-test (df = 1).

Species pool	Seed bank			Life form		
	Persistent	Transient	χ^2 statistics	Annuals	Perennials	χ^2 statistics
Regional flora	34.1 (140)	65.9 (270)	$\chi^2 = 29.574$, $p < 0.001$	36.0 (182)	64.0 (324)	$\chi^2 = 1.87$, ns
Nests	62.5 (50)	37.5 (30)		42.8 (36)	57.2 (48)	

Table 4. Percentages (numbers in parentheses) of species with different habitat requirements found in the regional flora and in the stork nests. Proportion of species in the regional pool was treated as the expected value in the χ^2-test (df = 1).

Species pool	Trophy			Light			Moisture		
	Rich (4–5)*	Poor to moderately poor (1–3)*	χ^2 statistics	Full to moderate (4–5)*	Shade (1–3)*	χ^2 statistics	Dry and fresh (1–3)*	Moist and wet (4–5)*	χ^2 statistics
Regional flora	31.0 (157)	69.0 (349)	$\chi^2 = 20.773$, $p < 0.001$	97.6 (494)	2.4 (12)	$\chi^2 = 0$, ns	87.9 (445)	12.1 (69)	$\chi^2 = 9.600$, $p < 0.01$
Nests	53.7 (44)	46.3 (38)		97.6 (80)	2.4 (2)		78.0 (64)	22.0 (18)	

* indicator value-ranges according to Zarzycki *et al.* (2002) in parentheses.

10% (Appendix 1). The most common exzoochorous mechanism was secretion of mucilage and seed adhesion, which are typical for some very abundant species (e.g., *Plantago major*, *Urtica dioica*, *Trifolium pratense* and *T. repens*).

Discussion

The ecological role of birds, especially in human-dominated landscapes, has recently become broadly appreciated. They are believed to perform the most diverse range of ecological functions among vertebrates: they are effective vectors in seed dispersal as well as ecological engineers by constructing nests (Sekercioglu 2006). The white stork, and probably some other birds as well, play both of these roles.

A widely known mechanism of seed dispersal mediated by birds is frugivory (e.g. McClanahan & Wolfe 1987, Debussche & Isenmann 1994, Adamowski & Knopik 1996, Nogales *et al.* 1999). Birds can be also one of the chain links in polichory, as are also the shrink *Lanius excubitor* and some lizards studied on the Canary Islands (Nogales *et al.* 1998, 2007). Some birds (the grey partridge *Perdix perdix*, the emu *Dromaius novaehollandiae*, the rook *Corvus frugilegus*) disperse seeds without any adaptations to frugivory, usually accidentally consuming seeds during food foraging (Calviño-Cancela *et al.* 2006, Orłowski & Czarnecka 2009, Czarnecka & Kitowski 2010). Sometimes the term “secondary dispersal” — a process by which seeds that are already on the ground are moved to another location — best describes this mechanism (Wang & Smith 2002). An unexpectedly high number of seeds without morphological adaptations to endozoochory is dispersed over long distances by migratory ducks; moreover, a vast majority of seeds is deposited in habitats suitable for germination and establishment (Brochet *et al.* 2009, 2010). Brochet *et al.* (2009) claimed that the absence of external adaptation for ornitochory in plant species found in the intestinal tract of the ducks was the reason for underestimating the significance of waterbirds in their dispersal. We can also say that since we cannot link any morphological adaptation of seeds to dispersal with nest material, the importance of the white stork and probably many other bird species was also overlooked, especially for species connected with agricultural landscape. Dispersal by the stork and possibility of establishment in the nests seems the most beneficial to weeds without any dispersal adaptation (prevailing in the nests), whose dispersal would otherwise be rather limited (Benvenuti 2007).

Unintentional seed dispersal during collection of nest material by birds is also a form of secondary dispersal. Seeds can be brought to white storks' nests together with dung, plant material and soil. Dean *et al*. (1990) found a large amount of seeds in the nests of 31 bird species in the semiarid karoo shrubland, and these seeds had been brought there with plant material serving as lining of the nests. On the other hand, soil was the source of seeds in the nests of the magpie *Pica pica* and a comparison of the structure of the seed pool in the nests and the vegetation in the vicinity of the nesting sites helped to identify the source of the nest material (Czarnecka & Kitowski 2008).

We were curious if it would be possible to identify the main source of the nest material of the white stork. Although we did not study the vegetation structure in the neighbourhood of the nests, we can point out a possible source. There are considerable similarities between the seed pool of the white stork nests and the seeds found in dung of vertebrate herbivores (Appendix 1). Thirty-four species — i.e. almost one third of all the taxa which germinated from the nest material (among them e.g. *Juncus bufonius*, *Poa annua*, *P. pratensis*, *Plantago major*, *Setaria pumila*, *Stellaria media*, *Trifolium pratense*, *T. repens* and *Urtica dioica*) — were also found in the dung of various herbivores (horse, cattle, sheep, white-tailed deer and rabbit). The share of the largest groups of species (e.g. graminoids, species with persistent seed banks; Cosyns & Hoffmann 2005) also points to herbivore dung as an important source of the nest material for the white stork and the source of seeds deposited in its nests. The white stork can thus act as a link in the multi-step dispersal chain and can also facilitate long-distance dispersal of some plant species, especially those with limited dispersal capabilities (i.e. mainly weeds with barochorous seeds). The same situation was observed for the dispersal mediated by large herbivores (Calviño-Cancela 2011).

Knowledge of seed-dispersal mechanisms must be combined with understanding of post-dispersal establishment. Not only does the white stork affect the transfer of propagules, but it also creates a specific habitat for germination and seedling establishment. It is thought that sometimes benefits of long-distance dispersal, or even dispersal over shorter distances, are balanced by e.g. failure to reach a suitable establishment site (Nathan *et al*. 2008). However, it does not seem to be true in our study. The white stork changes the environment by transforming non-living materials from one physical state to another. In this way, patches suitable for establishment and plant growth are created in nests. In such nutrient-rich habitat, plant species associated with fertile soils, which dominated in the seed pool, can germinate and grow very fast.

Behaviour of the white stork can explain high content of most macro- and microelements of the nest substratum (e.g. food is regurgitated onto the nest's floor by parents; Bocheński & Jerzak 2006). Rapid growth of stabilized plant individuals on the nest material was observed in our study in laboratory conditions and it was also noticed when germination from dung was studied (Mouisse *et al*. 2005). We think that the ecological role of dung depositions and nests of the white stork in temperate open habitats can be very similar. Both of them can be treated as sites with similar chemical properties (both are nutrient-rich) and similar seed-pool structures. As compared with dung, nests are more challenging habitats due to the presence of birds and the risk of drying.

Acknowledgements

We thank Prof. Andy J. Green for valuable remarks on the manuscript.

References

Adamowski, W. & Knopik, A. 1996: Ornitochorous species penetration onto abandoned farmland during secondary succession. — *Phytocoenosis* 8 *(Non Supplementum) Seminarium Geobotanicum* 4: 97–110.

Bakker, J. P., Bakker, E. S., Rosén, E., Verweij, G. L & Bekker, R. M. 1996: Soil seed bank composition along a gradient from dry alvar grassland to *Juniperus* shrubland. — *Journal of Vegetation Science* 7: 165–176.

Bartuszevige, A. M. & Endress, B. A. 2008: Do ungulates facilitate native and exotic plant spread? Seed dispersal by cattle, elk and deer in northeastern Oregon. — *Journal of Arid Environment* 72: 904–913.

Benvenuti, S. 2007: Weed seed movement and dispersal strategies in the agricultural environment. — *Weed Biology and Management* 7: 141–157.

Bocheński, M. & Jerzak, L. 2006: Behaviour of the white stork *Ciconia ciconia*: a review. — In: Tryjanowski, P., Sparks, T. H. & Jerzak, L. (eds.), *The white stork in Poland: studies in biology, ecology and conservation*: 295–324. Bogucki Sci. Publ., Poznań.

Brochet, A. L., Guillemain, M., Fritz, H., Gauthier-Clerc, M. & Green, A. J. 2009: The role of migratory ducks in the long-distance dispersal of native plants and the spread of exotic plants in Europe. — *Ecography* 32: 919–928.

Brochet, A. L., Guillemain, M., Fritz, H., Gauthier-Clerc, M. & Green, A. J. 2010: Plant dispersal by teal (*Anas crecca*) in the Camargue: duck guts are more important than their feet. — *Freshwater Biology* 55: 1262–1273.

Brown, J. H. 1995: Organisms as engineers: a useful framework for studying effects on ecosystems? — *Trends in Ecology and Evolution* 10: 51–52.

Cain, M. L., Milligan, B. G. & Strand, A. 2000: Long-distance seed dispersal in plant populations. — *American Journal of Botany* 87: 1217–1227.

Calviño-Cancela, M. 2011: Seed dispersal of alien and native plants by vertebrate herbivores. — *Biological Invasions* 13: 895–904.

Calviño-Cancela, M., Dunn, R. R., van Etten, E. J. B. & Lamont, B. B. 2006: Emus as non-standard seed dispersers and their potential for long-distance dispersal. — *Ecography* 29: 632–640.

Cosyns, E. & Hoffmann, M. 2005: Horse dung germinable seed content in relation to plant species abundance, diet composition and seed characteristics. — *Basic and Applied Ecology* 6: 11–24.

Chylarecki, P., Jawińska, D. & Kuczyński, L. 2006: *Monitoring pospolitych ptaków lęgowych. Raport z lat 2003–2004*. — OTOP, Warszawa.

Czarnecka, J. & Kitowski, I. 2008: The potential role of nests of black-billed magpie *Pica pica* L. in accumulation and dispersal of seeds in agricultural landscape. — *Polish Journal of Ecology* 56: 673–682.

Czarnecka, J. & Kitowski, I. 2010: Seed dispersal by the Rook *Corvus frugilegus* L. in agricultural landscape – mechanisms and ecological importance. — *Polish Journal of Ecology* 58: 511–523.

Czarnecka, J., Kitowski, I., Orłowski, G. & Sugier, P. 2010: Non-standard mechanisms of seed dispersal in agricultural landscape — the role of white stork, grey partridge and rook. — *Acta Societatis Botanicorum Poloniae* 79 *(Supplementum 1)*: 36.

Davies, A. & Waite, S. 1998: The persistence of calcareous grassland species in the soil seed bank under developing and established scrub. — *Plant Ecology* 136: 27–39.

Dean, W. R., Milton, S. J. & Siegfried, W. R. 1990: Dispersal of seeds as nest material by birds in semiarid karoo shrubland. — *Ecology* 7: 1299–1306.

Debussche, M. & Isenmann, P. 1994: Bird dispersed seed rain and seedling establishment in patchy Mediterranean vegetation. — *Oikos* 69: 414–426.

Drezner, T. D., Fall, P. L. & Stromberg, J. C. 2001: Plant distribution and dispersal mechanisms at the Hassayampa River Preserve, Arizona, USA. — *Global Ecology and Biogeography* 10: 205–217.

Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W. & Paulissen D. 1991: Zeigerwerte von Pflanzen in Mitteleuropa. — *Scripta Geobotanica* 18: 1–248.

Grime, J. P., Hodgson, J. G. & Hunt, R. 1996: *Comparative plant ecology. A functional approach to common British species*. — Chapman & Hall, London.

Guziak, R. & Jakubiec, Z. (eds.) 2006: *White stork Ciconia ciconia L. in Poland in 2004. Results of the VIth International White Stork Census*. — PTPP "pro Natura", Wrocław.

Hansell, M. H. 1993: The ecological importance of animal nests and burrows. — *Functional Ecology* 7: 5–12.

Indykiewicz, P. 2006: House sparrow *Passer domesticus*, starling *Sturnus vulgaris*, tree sparrow *Passer montanus* and other residents of nests of the white stork *Ciconia ciconia*. — In: Tryjanowski, P., Sparks, T. H. & Jerzak, L. (eds.), *The white stork in Poland: studies in biology, ecology and conservation*: 225–235. Bogucki Sci. Publ., Poznań.

Iravani, M., Schutz, M., Edwards, P. J., Risch, A. C., Scheidegger, C. & Wagner, H. H. 2011: Seed dispersal in red deer (*Cervus elaphus* L.) dung and its potential importance for vegetation dynamics in subalpine grasslands. — *Basic and Applied Ecology* 12: 505–515.

IUNG 1990: *Fertilizer recommendations. Border values for evaluation of macro- and microelements content in soils*, 2nd ed. — IUNG Scientific Publishing Department, Puławy.

Jones, C. G., Lawton, J. H. & Shachak, M. 1994: Organisms as ecosystem engineers. — *Oikos* 69: 373–386.

Jones, C. G., Lawton, J. H. & Shachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. — *Ecology* 78: 1946–1957.

Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., Poschold, P., van Groenendael, J. M., Klimeš, L., Klimešova, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J. G., Jackel, A. K., Kühn, I., Kunzmann, D., Ozinga, W. A., Römermann, C., Stadler, M., Schlegmilch, J., Steendam, H. J., Tackenberg, O., Wilmann, B., Cornelissen, J. H. C., Eriksson, O., Garnier, E. & Peco, B.. 2008: The LEDA Traitbase: a database of life-history traits of northwest European flora. — *Journal of Ecology* 96: 1266–1274.

Kosicki, J. Z., Sparks, T. & Tryjanowski, P. 2007: House sparrows benefit from the conservation of white storks. —*Naturwissenschaften* 94: 412–415.

Koutecká, E. & Lebš, J. 2009: Effect of light and moisture conditions and seed age on germination of three closely related *Myosotis* species. — *Folia Geobotanica* 44: 109–130.

Laland, K. N. & Boogert, W. J. 2010: Niche construction, co-evolution and biodiversity. — *Ecological Economics* 69: 731–736.

Leck, M. A. & Schutz, W. 2005. Regeneration of Cyperaceae, with particular reference to seed ecology and seed banks. — *Perspectives in Plant Ecology, Evolution and Systematics* 7: 95–133.

Łomnicki, A. 2011: *Wprowadzenie do statystyki dla przyrodników.* — PWN, Warszawa.

Matus, G., Papp, M. & Tothemresz, B. 2005: Impact of management on vegetation dynamics and seed bank formation of inland dune grassland in Hungary. — *Flora* 200: 296–306.

McClanahan, T. R. & Wolfe, R. W. 1987: Dispersal of ornithochorous seeds from forest edges in central Florida. — *Vegetatio* 71: 107–112.

Mirek, Z., Piękoś-Mirkowa, H., Zając, A. & Zając, M. 2002: *Flowering plants and pteridophytes of Poland. A checklist.* — W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.

Mouissie, A. M., Vos, P., Verhagen, H. M. C. & Bakker, J. P. 2005: Endozoochory by free ranging, large herbivores: Ecological correlates and perspectives for restoration. — *Basic and Applied Ecology* 6: 547–558.

Myers, J. A., Vellend, M., Gardescu, S. & Marks, P. L. 2004: Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. — *Oecologia* 139: 35–44.

Nathan, R., Schurr, F. M., Spiegel, O., Steinitz, O., Trakhtenbrot, A. & Tsoar, A. 2008: Mechanisms of long-distance seed dispersal. — *Trends in Ecology and Evolution* 23: 638–647.

Nogales, M., Delgado, J. D. & Medina, F. M. 1998: Shrikes, lizards and *Lycium intricatum* (Solanaceae) fruits: a case of indirect seed dispersal on an oceanic island (Alegranza, Canary Islands). — *Journal of Ecology* 86: 866–871.

Nogales, M., Hernández, E. C. & Valdés, F. 1999: Seed dispersal by common ravens *Corvus corax* among island habitats (Canarian Archipelago). — *Ecoscience* 6: 56–61.

Nogales, M., Padilla, D. P., Nieves, C., Illera, J. C. & Traveset, A. 2007: Secondary seed dispersal system, frugivorous lizards and predatory birds in insular volcanic badlands. — *Journal of Ecology* 95: 1394–1403.

Nowakowski, J. J. 2006: The influence of weather and intrapopulation competition on breeding success of the white stork *Ciconia ciconia* population in the southern basin of the Biebrza river valley. — In: Tryjanowski, P., Sparks, T. H. & Jerzak, L. (eds.), *The white stork in Poland: studies in biology, ecology and conservation*: 143–160. Bogucki Sci. Publ., Poznań.

Orłowski, G. & Czarnecka, J. 2009: Granivory of birds and seed dispersal: viable seeds of *Amaranthus retroflexus* L. recovered from the droppings of the grey patridge *Perdix perdix* L. — *Polish Journal of Ecology* 57: 191–196.

Pakeman, R. J., Digneffe, G. & Small, J. L. 2002: Ecological correlates of endozoochory by herbivores. — *Functional Ecology* 16: 296–304.

Palisaar, J. 2006: *The floodplain meadows of Soomaa, National Park, Estonia. Vegetation-dispersal-regeneration.* — Ph.D. thesis, Regensburg University.

Sekercioglu, C. H. 2006: Increasing awareness of avian ecological function. — *Trends in Ecology and Evolution* 21: 464–471.

Stanisz, A. 1998: *Przystępny kurs statystyki.* — StatSoft Polska Sp. z o.o., Kraków.

Thompson, K., Bakker, J. P. & Bekker, R. M. 1997: *The soil seed banks of North West Europe: methodology, density and longevity.* — University Press, Cambridge.

Tryjanowski, P., Kuźniak, S., Kujawa, K. & Jerzak, L. 2009: *Ekologia ptaków krajobrazu rolniczego.* — Bogucki Sci. Publ., Poznań.

Tryjanowski, P., Sparks, T. H. & Profus, P. 2005: Uphill shifts in distribution of the white stork *Ciconia ciconia* in southern Poland: the importance of nest quality.— *Diversity Distribution* 11: 219–223.

Williams, S. C., Ward, J. S. & Ramakrishnan, U. 2008: Endozoochory by white-tailed deer (*Odocoileus virginianius*) across a suburban/woodland interface. — *Forest Ecology and Management* 255: 940–947.

Wright, J. P. & Jones, C. G. 2006: The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. — *BioScience* 56: 203–209.

Wang, B. C. & Smith, T. B. 2002: Closing the seed dispersal loop. — *Trends in Ecology and Evolution* 17: 379–385.

Zając, A. & Zając, M. 2001: *Atlas rozmieszczenia roślin naczyniowych w Polsce.* — Laboratory of Computer Chorology, Institute of Botany, Jagiellonian University and Foundation of Jagiellonian University, Kraków.

Zarzycki, K., Trzcińska-Tacik, H., Szeląg, Z., Wołek, J. & Korzeniak U. 2002: *Ecological indicator values of vascular plants of Poland.* — W. Szafer Institute of Botany, Polish Academy of Science, Kraków.

Zawadzki, S. 1999: *Gleboznawstwo.* — PWRiL, Warszawa.

Appendix 1. Structure of the seed bank of the white stork nests (*n* = 10). Mean number of seeds per 10 000 g of soil dry weight. Habitats: W = weeds and ruderal species; M = meadow and grassland species; PB = peat bog and rush species; O = other species. Life forms: A = annuals; P = perennial herbs; W = woody species and shrubs. Dispersal modes: B = barochory (no obvious dispersal adaptations); A = anemochory; Ex = exozoochory, En = endozoochory, M = myrmecochory, H = hydrochory. Seed bank types: T = transient; P = persistent; ND = not determined. Nomenclature according to Mirek *et al.* (2002).

Taxa	Mean number of seedlings	Number of occurences	Habitat	Life form	Dispersal mode	Seed bank
Chenopodium album[5]	183	10	W	A	B	P
Urtica dioica[1,2,3,4,6]	86	8	W	P	Ex	P
Polygonum lapathifolium subsp. *pallidum*[5]	51	5	W	A	B	P
Poa annua[1,2,3,4,5,6]	50	10	W	A	B	P
Plantago major[1,4,5,6]	48	8	W	P	Ex	P
Poaceae	48	8	–	–	–	–
Poa pratensis[1,2,3,4,5]	47	8	M	P	B	P
Polygonum aviculare	37	7	W	A	B	P
Trifolium pratense[5,6]	25	8	M	P	Ex	T
Deschampsia caespitosa[4]	24	6	M	P	Ex	T
Setaria pumila	17	7	W	A	B	P
Juncus bufonius[1,2,3,4]	15	6	O	A	Ex	P
Elymus repens[5]	12	4	W	P	B	P
Medicago lupulina[1,4,5]	12	10	W	A	B	T
Trifolium repens[1,3,4,5,6]	12	7	M	P	Ex	T
Anethum graveolens	12	1	O	A	B	ND
Artemisia vulgaris[5]	10	3	W	P	B	P
Conyza canadensis	9	4	W	A	B/Ex	P
Stellaria media[1,2,3,4,5]	9	8	W	A	B	P
Amaranthus retroflexus[5]	8	4	W	A	B	P
Capsella bursa-pastoris[1,5]	8	6	W	A	A	P
Fallopia convolvulus	8	6	W	A	B	P
Galinsoga parviflora	8	8	W	A	A	P
Carex hirta	7	5	W	P	B	T
Echinochloa crus-galli	7	5	W	A	B	P
Daucus carota	7	1	M	P	Ex	P
Arctium tomentosum	5	2	W	P	Ex	T
Leonurus cardiaca	5	2	W	P	Ex	ND
Melandrium album	5	5	W	A	B	T
Ballota nigra	4	2	W	P	Ex	P
Gypsophila muralis	4	1	W	A	B	P
Viola arvensis	4	5	W	A	M	P
Agrostis sp.	4	3	–	–	–	–
Carex sp.	4	3	–	–	–	–
Polygonum minus	3	1	W	A	B	ND
Rumex crispus[1]	3	5	W	P	B	P
Veronica arvensis[1,4]	3	1	W	A	B	T
Alopecurus pratensis	3	3	M	P	B	T
Veronica chamaedrys[1,2,3,4,6]	3	3	M	P	B	T
Juncus conglomeratus	3	1	PB	P	Ex	P
Bidens tripartitus	3	2	O	A	Ex/H	P
Rumex sp.	3	3	–	–	–	–
Apera spica-venti	2	2	W	A	Ex	P
Chenopodium hybridum	2	1	W	A	B	P
Glechoma hederacea[4]	2	4	W	P	B	T
Polygonum persicaria[5]	2	3	W	A	B	P
Potentilla reptans[1]	2	1	W	P	B	T

continued

Appendix 1. Continued.

Taxa	Mean number of seedlings	Number of occurences	Habitat	Life form	Dispersal mode	Seed bank
Ranunculus repens[1,3,4]	2	4	W	P	H/Ex	P
Vicia hirsuta	2	1	W	A	B	T
Lythrum salicaria[1,4,5]	2	3	M	P	H	T
Scirpus sylvaticus	2	2	M	P	H	T
Agrostis capillaris[1,3,4]	2	2	PB	P	B	P
Epilobium sp.	2	3	–	–	–	–
Fabaceae	2	2	–	–	–	–
Juncus sp.	2	1	–	–	–	–
Anagallis arvensis	1	2	W	A	B	P
Chamomilla suaveolens	1	3	W	A	B	P
Chenopodium polyspermum	1	1	W	A	B	P
Galium boreale	1	1	M	P	B	T
Geranium pusillum	1	1	W	A	B	P
Lamium amplexicaule	1	1	W	A	B	P
Melilotus alba/officinalis[5]	1	2	W	A	B	T
Rumex acetosella[1,3,4]	1	1	W	A	B	P
Rumex obtusifolius[3,4]	1	1	W	P	Ex	P
Betonica officinalis	1	2	M	P	B	T
Coronilla varia[5]	1	1	M	P	B	P
Holcus lanatus[1,3,4]	1	1	M	P	B	P
Hypericum perforatum	1	1	M	P	A	P
Lolium perenne[1,3,4]	1	2	M	P	B	T
Peucedanum palustre	1	1	M	P	H	T
Plantago lanceolata[1]	1	1	M	P	Ex	P
Poa trivialis[1,3,4]	1	2	M	P	B	P
Taraxacum officinale[5]	1	2	M	P	A	T
Vicia sepium	1	1	M	P	B	T
Carex acutiformis	1	1	PB	P	H	P
Lycopus europaeus[1,4]	1	3	PB	P	H	T
Geranium sp.	1	2	–	–	–	–
Petroselinum crispum	1	1	O	P	–	–
Rubus sp.	1	1	–	P	En	ND
Sambucus nigra	1	1	O	W	En	P
Verbascum sp.	1	1	–	–	–	–
Veronica sp.	1	1	–	–	–	–
Artemisia absinthium	< 1	1	W	P	B	P
Centaurea cyanus	< 1	1	W	A	A	P
Galium aparine[1]	< 1	1	W	A	Ex	T
Gnaphalium luteo-album	< 1	1	W	A	A	ND
Sonchus asper[5]	< 1	1	W	A	A	P
Dactylis glomerata[4,5,6]	< 1	1	M	P	B	T
Lysimachia vulgaris[1]	< 1	1	M	P	H	T
Myosotis palustris	< 1	1	M	P	B	P
Ranunculus acris	< 1	1	M	P	Ex	T
Rumex acetosa[3,4]	< 1	1	M	P	A	T
Symphytum officinale	< 1	1	M	P	H/A	T
Veronica beccabunga	< 1	1	PB	P	H	P
Atriplex sp.	< 1	1	–	–	–	–
Barbarea vulgaris	< 1	1	O	P	A	P
Betula pendula	< 1	1	O	W	A	P
Non-identified	1	1	–	–	–	–

Species present in animal dung: [1] horse (Cosyns & Hoffmann 2005, Mouissie *et al.* 2005), [2] rabbit (Pakeman *et al.* 2002), [3] sheep (Pakeman *et al.* 2002, Mouissie *et al.* 2005), [4] cattle (Mouissie *et al.* 2005, Bartuszevige & Endress 2008), [5] white-tailed deer (Myers *et al.* 2004, Williams *et al.* 2008), [6] red deer (Iravani *et al.* 2011).

Appendix 2. Physicochemical properties of the material from the white-stork nests.

Soil property	Nest number									
	1	2	3	4	5	6	7	8	9	10
pH										
1 M KCl	4.87	4.52	4.51	4.96	4.96	5.1	4.32	5.88	5.15	4.75
Nest material reaction[a]	acidic	acidic	acidic	acidic	acidic	acidic	highly acidic	moderately acidic	acidic	acidic
Macro-elements										
N (g kg^{-1})[b]	19.9	24.7	14.3	14.5	13.8	13.3	19.3	17.2	22.5	14.0
C/N	8.94	8.81	7.66	8.70	8.24	10.05	9.46	7.88	7.31	9.01
P_2O_5 (mg per 100 g)	463.5	259.5	180.0	130.0	219.5	314.5	379.5	378.0	386.0	344.0
P content[c]	very high	very high	very high	very high	very high	very high	very high	very high	very high	very high
K_2O (mg per 100 g)	250.0	142.0	118.5	103.5	59.5	84.0	162.0	150.0	82.5	62.5
K content[c]	very high	very high	high	high	low/ medium	medium	very high	very high	medium	medium
Mg (mg per 100 g)	49.0	31.5	35.5	21.0	24.0	41.05	31.0	45.0	37.5	35.5
Mg content[c]	medium	low	low	low	low	medium	low	medium	low	low
Micro-elements										
Cu (mg per 1000 g)	6.01	5.46	8.09	11.47	12.39	15.1	16.9	26.6	16.1	13.34
Cu content[c]	medium	low	medium	medium/ high	high	high	high	high	high	high
Zn (mg per 1000 g)	59.4	64.1	58.0	46.0	47.2	80.9	96.0	70.5	82.7	53.8
Zn content[c]	high	high	high	high	high	high	high	high	high	high
Mn (mg per 1000 g)	189.6	108.6	92.2	98.1	76.6	159.3	182.8	227.5	104.9	92.6
Mn content[d]	medium	medium	medium	medium	medium	medium	medium	medium	medium	medium
Fe (mg per 1000 g)	896	422	412	516	420	541	1006	1479	569	2764
Fe content[d]	medium	low	low	low	low	low	medium	medium	low	medium

[a] scale for all soil types (IUNG 1990); [b] For comparison, total N content in Polish soils ranges from 0.2 to 3.5 g kg^{-1} (Zawadzki 1999); [c] scale for organic soils (IUNG 1990); [d] scale for mineral soils (IUNG 1990).