Food in a row: urban trees offer valuable floral resources to pollinating insects

Laurent Somme[1] · Laura Moquet[1] · Muriel Quinet[1] ·
Maryse Vanderplanck[2] · Denis Michez[2] ·
Georges Lognay[3] · Anne-Laure Jacquemart[1]

Abstract Urbanization affects the availability and diversity of floral resources (pollen and/or nectar) for wild pollinating insects. For example, urban green areas are characterized by an abundance of ornamental plant species. Increasingly, trees are planted to improve the aesthetics of urban streets and parks. These urban trees might offer important floral resources to pollinating insects. To examine the suitability of urban trees as resources for pollinating insects, we investigated the chemical composition of pollen and nectar as well as the amount of nectar produced by the nine major insect-pollinated tree species planted in cities of Western Europe, namely *Acer pseudoplatanus*, *Aesculus carnea*, *A. hippocastanum*, *Robinia pseudoacacia*, *Tilia cordata*, *T.* x *euchlora*, *T.* x *europaea*, *T. platyphyllos* and *T. tomentosa*. The analyses revealed that globally the *Tilia* trees provide pollen with lower contents of polypeptides, amino acids and phytosterols compared with the other species. Urban tree flowers offer abundant nectar with relatively high sugar contents (0.16–1.28 mg/flower); sucrose was the predominant sugar in all nectars. The investigated tree species could therefore be considered in future city plantings.

✉ Anne-Laure Jacquemart
anne-laure.jacquemart@uclouvain.be

[1]   Earth and Life Institute, Research Group Genetics, Reproduction, Populations, Université catholique de Louvain, Croix du Sud 2, Box L7 05 14, 1348, Louvain-la-Neuve, Belgium

[2]   Laboratory of Zoology, Research Institute of Biosciences, Université de Mons, Place du Parc 23, 7000 Mons, Belgium

[3]   Laboratory of Analytical Chemistry, Gembloux Agro-Bio Tech, Université de Liège, Passage des Déportés 2, 5030 Gembloux, Belgium

Introduction

Urban areas are expanding worldwide, altering or even destroying natural habitats (Matteson and Langellotto 2010). The changes in habitats associated with urbanization often modify the composition and abundance of animal and plant communities. Because insect pollinating species usually require particular food resources (pollen and nectar) and breeding sites, urbanization can compromise their needs (Goulson 2009; Potts et al. 2010a). Urbanization can increase or decrease species richness, depending on several variables like intensity of urbanization, taxonomic group, spatial scale of analysis or food specialization. Urban areas might be suitable habitats for pollinating species, especially generalist species that forage on different plant resources (Goulson et al. 2002; Hernandez et al. 2009; Winfree et al. 2009; Baldock et al. 2015). For instance, studies showed a positive effect of urbanization on the total numbers of several bee species (Everaars et al. 2011; Sirohi et al. 2015). Nevertheless, in other cases, urbanization induces negative effects on pollinator assemblages by reducing pollinator abundance or diversity (McKinney 2008; Bates et al. 2011). Because urbanization generally leads to the loss of native plants in both cover and diversity, gardens, parks, wastelands and street environments sustain different floral resources than do natural habitats, with diverse and sometimes abundant exotic species (Collins et al. 2000; Frankie et al. 2005; Banaszak-Cibicka and Żmihorski 2012). The effect of these exotic plant species on insects depend on plant species: some do not provide floral resources (Comba et al. 1999a; Corbet et al. 2001), whereas others provide resource for native insects as good as or better than native species (Frankie et al. 2005; Acar et al. 2007; Vervoort et al. 2011; Cawoy et al. 2012; Hanley et al. 2014; Salisbury et al. 2015). In particular, entomophilous exotic urban trees might provide supplemental food resources for pollinating insects by producing thousands of flowers per tree (Kevan 1990; Hunter and Hunter 2008). For instance, trees of *Acer rubrum* (Aceraceae) generate approximately 1350 flowers/m^3 (Batra 1985), whereas trees of *Tilia* species (Tiliaceae) develop up to 2400 flowers/m^2 (Baude et al. 2016). Urban tree plantations are usually dominated by only a few species with short blooming periods (Pauleit et al. 2002; Sjöman et al. 2012b) and pollinating insects are therefore confronted with spatio-temporal disparities in floral resources (i.e. abundance and diversity). Because eusocial bees require large amounts of nectar and pollen throughout the colony's active period (approximately from April to September), they might be particularly affected by inadequate nutrition intake related to gaps in flower availability or quality (Goulson et al. 2002; Potts et al. 2010a; Couvillon et al. 2014). In the context of urban beekeeping (i.e. the increase in urban beehives; Alton and Ratnieks 2013), a shortage of entomophilous plants might strengthen competition between honey bees and other pollinating insects (Thomson 2004; Goulson and Sparrow 2008) and/or lead to a collapse in urban populations of honey bees and honey production (Potts et al. 2010b).

Pollinating insects use nectar and/or pollen from foraged plants as nutrient resources (Goulson and Darvill 2004). Nectar serves as an energy source while pollen is the major nutrient resource used for the development of larvae (Roulston and Cane 2000; Génissel et al. 2002; Cnaani et al. 2006; Nicolson 2011). Nectar consists mainly of sugars (Corbet 2003; Gonzalez-Teuber and Heil 2009). Pollen consists mostly of lipids (including phytosterols) and nitrogen compounds (Roulston and Cane 2000). Nectar and pollen chemical composition are highly variable among plant species (Roulston and Cane 2000; Génissel et al. 2002; Cnaani et al. 2006; Kitaoka and Nieh 2009; Nicolson 2011). Importance of plant species for pollinating insects will thus depend both on the abundance and chemical quality of their floral

resources. Studies of floral resources and pollinators traditionally have focused on flower strips (Haaland and Gyllin 2010; Matteson and Langellotto 2010; Gunnarsson and Federsel 2014), urban gardens (Comba et al. 1999b; Pawelek et al. 2009; Haaland and Gyllin 2010; Garbuzov and Ratnieks 2014; Gunnarsson and Federsel 2014), parks (McFrederick and Le Buhn 2006; Wojcik et al. 2008) and allotments (Ahrné et al. 2009). The potential of urban trees as floral resources for insects has been overlooked, and tree pollen nutritional quality has not been investigated. Several species of trees have been widely planted in urban areas in Western Europe (Sjöman et al. 2012a), including *Acer pseudoplatanus* and *A. platanoides* (maple trees, Aceraceae), *Aesculus hippocastanum* and *A. carnea* (horse chestnut trees, Hippocastanaceae), *Robinia pseudoacacia* (black locust, Fabaceae) and several *Tilia* species (linden or lime trees, Tiliaceae). In Belgium, the collective flowering periods of these tree species last from mid-April to mid-August with overlap of the flowering periods of the individual species (Lambinon and Verloove 2012; Fig. 1). Therefore, these trees could be an important nutritional resource for bees during the period of nesting and colony development (Dicks et al. 2015).

The present study focuses on urban trees in Brussels, Belgium. Green areas (i.e. gardens, parks, wastelands, woodlands) cover half of the city (i.e. 8000 ha) with an uneven distribution, from 10 % in the inner historical centre to 70 % in the suburbs (Bruxelles Environnement 2003). Trees are planted along the majority of streets and roads. For example, along 350 km of 'regional' roads, more than 27,000 trees belonging to 140 species are planted. Approximately 66.5 % of all planted trees belong to only four genera: *Platanus* (22 %; wind-pollinated species, Tedeschini et al. 2006), *Tilia* (18 %), *Acer* (14 %) and *Aesculus* (13 %; V. Decoux, pers. comm.). In urban areas, honey bees and bumble bees are the main visitors of the majority of trees from the *Acer*, *Aesculus*, *Robinia* and *Tilia* genera (Williams et al. 1993; Pawlikowski 2010; Weryszko-Chmielewska et al. 2012; Cierjacks et al. 2013).

Recently, Vaudo et al. (2015) proposed that a step to restore and conserve the habitats of pollinating insects is to determine the nutritional requirements of different insect species as well as the nutritional quality of pollen and nectar from host-plant species. Here, we focused on nutritional quality, knowledge of which is essential to predict the effect of urban trees on the abundance and diversity of pollinating insects. To estimate the potential floral resources for insect visitors, we performed a study of the pollen and nectar chemical composition, as well as nectar quantification, in the main entomophilous urban trees in Brussels, namely *Acer pseudoplatanus*, *Aesculus carnea*, *A. hippocastanum*, *Robinia pseudoacacia*, *Tilia cordata*, *T.* x *euchlora*, *T.* x *europaea*, *T. platyphyllos* and *T. tomentosa*.

Fig. 1 Phenology of the nine studied urban trees in Brussels, Belgium (adapted from Lambinon and Verloove 2012)
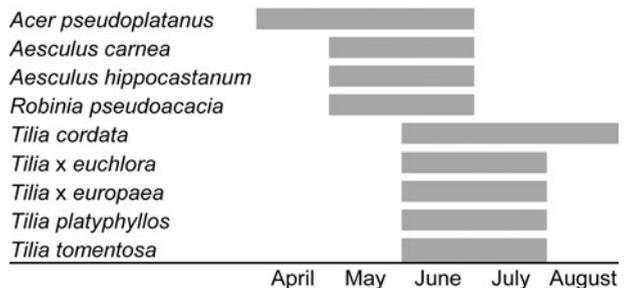
Materials and methods

Plant species

We sampled nine entomophilous urban tree species planted in Brussels, Belgium: *Acer pseudoplatanus* (Aceraceae), *Aesculus carnea* and *A. hippocastanum* (Hippocastanaceae), *Robinia pseudoacacia* (Fabaceae) and five *Tilia* (Tiliaceae) species (*Tilia cordata*, *T.* x *euchlora*, *T.* x *europaea*, *T. platyphyllos* and *T. tomentosa*). *Tilia* x *euchlora* is the hybrid between *T. cordata* and *T. dasystyla*. *Tilia* x *europaea* is the hybrid between *T. cordata* and *T. platyphyllos* (Lambinon and Verloove 2012). *Tilia* trees were sampled along Avenue Val Duchesse, Avenue de la Chapelle, Avenue de Tervuren, Boulevard du Souverain, Boulevard Frans van Kalken, Boulevard Aristide Briand, Place du Conseil and Rue Eugène Toussaint. *Aesculus* species were sampled along Avenue Baron d'Huart, Avenue Berrewaert, Avenue Commandant Vander Meeren, Avenue du Parc de la Woluwe, Avenue du Roi Soldat, Avenue de Tervuren, Boulevard Félix Paulsen and Boulevard Eugène Ysaÿe. *Acer pseudoplatanus* was sampled along Avenue des Casernes, Avenue de Luttre, Avenue Molière, Avenue Reine Marie-Henriette, Avenue des Volontaires, Boulevard Industriel and Boulevard Edmond Machtens. *Robinia pseudoplatanus* was sampled along Avenue du Grand Hospice, Avenue Paepsem and Avenue Paul Héger.

Pollen composition

Pollen sampling

At the peak of flowering (i.e. between late April and late July 2013; Fig. 1), branches with unopened flower buds were harvested from a minimum of five trees for each species. Branches, placed in tap water, were kept for one night at room temperature (approx. 20 °C) in the laboratory. On the next morning, stamens were extracted from newly opened flowers. Stamens were stored at −20 °C and subsequently dried at room temperature for 12 h before pollen was removed using a sieve (Sieve 3″, Brass-Stainless, Full Height, 80 μm). Pure pollen samples were pooled to obtain 200 mg samples sufficient for analyses and stored at −20 °C until use. All chemical analyses were performed in triplicate, as in other recent studies (Weiner et al. 2010; Somme et al. 2015; Villette et al. 2015).

Chemical analyses

The polypeptide content (molecular weight > 10,000 Da) in 5 mg dry pollen for each species ($n = 3$) was quantified following the method described in Vanderplanck et al. (2014a). The quantification of total polypeptides was performed using the bicinchoninic acid (BCA) Protein Assay Kit (Pierce, Thermo Scientific), and bovine serum albumin (BSA) was used for a standard curve.

The amino acid content in 3 mg dry pollen for each species ($n = 3$) was quantified following the method described in Vanderplanck et al. (2014b). Each amino acid, with the exception of tryptophan, was measured separately with ion exchange chromatography (Biochrom 20 plus amino acid analyser) using a post-column ninhydrin reaction and norleucine as an internal standard (University of Liège, Gembloux Agro-Bio Tech, Belgium). Due to technical problems, we were unable to determine cysteine and methionine contents for *Robinia pseudoacacia* and *Tilia platyphyllos*.

The phytosterol content in 15 mg dry pollen was quantified for each species ($n = 3$) following the method described in Vanderplanck et al. (2011). The total phytosterol content was determined by considering all quantifiable peaks of sterols that eluted between cholesterol and betulin (internal standard) (University of Liège, Gembloux Agro-Bio Tech, Belgium). Identifications were achieved by comparing the relative retention times (β-sitosterol–TMS = 1.00) with those of sunflower oil reference.

Chemical composition of nectar

Nectar sampling

Branches with unopened flower buds were harvested from a minimum of five trees for each species at the same time that pollen was collected. Nectar collection from flowers on the branches was conducted in the laboratory. Branches, placed in tap water, were kept for one night at room temperature (approx. 20 °C). On the next morning, nectar was extracted from newly opened flowers. This method avoids differences due to climatic conditions (temperature and relative humidity) in the field and previous visits to flowers by insects. Anthers and stigmas were removed from the flowers to improve accessibility to the nectar and to avoid pollen contamination. For each tree species, nectar was collected from at least 50 (depending on the nectar volume) newly opened flowers with glass capillary tubes of 1 μL or 5 μL (Hirschmann®Laborgerate, Eberstadt, Germany). The nectar volume was estimated by measuring the length of the nectar column in the capillary tube.

Chemical analyses

Nectar samples were stored at −80 °C until analyses of sugar concentration and composition. Sugar composition was determined on pooled samples by gas chromatography, with a Perkin-Elmer Autosystem XL equipped with a split injector (1/20) and helium as the carrier gas (flow of 1 ml/min). The injector and detector temperatures were maintained at 250 °C and 350 °C, respectively. Analyses for nectar composition were performed in the Centre Apicole de Recherche et d'Information (CARI asbl, Louvain-la-Neuve, Belgium). To determine the total sugar content of nectar per flower, sugar concentration was converted to mg/μl according to the formula: $y = 0.00226 + (0.00937 \ x) + (0.0000585 \ x^2)$ where y = sugar concentration (mg/μl) and x = sugar concentration (%) (Dafni et al. 2005). The total sugar content of nectar per flower (mg) was then calculated as volume of nectar (μl) x sugar concentration (mg/μl).

Data analyses

Prior to analyses of variance (ANOVA), homoscedasticity and normality were checked using Bartlett and Shapiro tests, respectively. One-way analyses of variance (ANOVA) were used to compare phytosterol content among tree species. As assumption violations occurred even after transformations for nectar volume, amino acid and polypeptide contents, we performed Kruskal-Wallis tests (i.e. data set with deviation from homoscedasticity regardless of normality).

To detect differences in pollen composition (i.e. amino acid and sterol profiles, expressed as μg/mg) and nectar composition (i.e. sugar profiles, expressed as μg/mg), we conducted perMANOVA (Bray-Curtis dissimilarity index, 999 permutations, "adonis" command) and multiple pairwise comparisons with Bonferroni's adjustment after testing for multivariate homogeneity ("betadisper"

command) (R-package *vegan*; Oksanen et al. 2013). Differences in nectar composition among species were visually assessed on UPGMA (unweighted pair group method with arithmetic mean) clusters using the Bray-Curtis dissimilarity index. We estimated the uncertainty in hierarchical cluster analysis with *p*-values calculated using multiscale bootstrap resampling (R-package *pvclust*; Suzuki and Shimodaira, 2006). Differences in chemical compositions (phytosterols and essential amino acids) among the different pollen sources were visually assessed using a non-metric multidimensional scaling (nMDS) ordination based on the Bray-Curtis similarity matrix with two dimensions (R-package *vegan*). Statistics were calculated in R using functions from *ecodist* (Goslee and Urban 2007). All analyses were conducted in R version 3.0.2 (R Development Core Team 2013).

Results

Chemical composition of pollen

Tree species produced pollen with polypeptide contents ranging from 21.0 ± 2.8 µg/mg (*Tilia cordata*) to 89.8 ± 11.6 µg/mg (*Aesculus carnea*). Pollen from *Tilia* species contained the lowest amounts of polypeptides, differing significantly from *Acer pseudoplatanus* and *Aesculus carnea* ($\chi^2 = 91.42$, df = 8, $p < 0.001$; Table 1).

Robinia pseudoacacia pollen contained the highest total amino acid content (375.1 ± 2.4 µg/mg), whereas *T. tomentosa* pollen contained the lowest (209.3 ± 5.6 µg/mg, $\chi^2 = 23.99$, df = 8, $p = 0.002$; Table 1). The analyses of amino acid similarities among tree species showed that the pollen samples were grouped according to taxa (Fig. 2a). All species of *Tilia* except *T. platyphyllos* were grouped together, likely due to their lower content in all amino acids except phenylalanine and cysteine compared to the other species ($p < 0.001$; Fig. 2a and Table 1). Despite the variation in amino acid composition among the studied tree species (perMANOVA, $F_{8,18} = 55.98$, $p = 0.001$), all tree pollen contained the full spectrum of essential amino acids (Online Resource 1).

According to the phytosterolic composition, all *Tilia* species, including *T. platyphyllos*, were grouped together (Fig. 2b). Total phytosterol concentration in pollen was lower in *Tilia* species (<

Table 1 Polypeptide, total amino acid, and sterol content (µg/mg; mean ± SD) in pollen from the nine studied tree species

Species	Polypeptide content (µg/mg)	Amino acid content (µg/mg)	Sterol content (µg/mg)
Acer pseudoplatanus	71.0 ± 11.1 [a]	290.2 ± 26.6 [ab]	9.04–13.74[a]
Aesculus carnea	89.8 ± 11.6 [a]	318.2 ± 8.5 [ab]	3.90–9.48[ab]
Aesculus hippocastanum	39.5 ± 7.0[abc]	331.7 ± 27.1 [ab]	4.93–5.07[b]
Robinia pseudoacacia	48.2 ± 5.1 [ab]	375.1 ± 2.4 [a]	9.99–10.35[ab]
Tilia cordata	21.0 ± 2.8 [d]	243.1 ± 13.2 [ab]	3.39–4.97[b]
Tilia x *euchlora*	36.3 ± 1.3[abcd]	243.9 ± 0.8 [ab]	2.59–7.00[b]
Tilia x *europaea*	33.4 ± 4.6[bcd]	260.6 ± 8.4 [ab]	2.82–5.41[b]
Tilia platyphyllos	26.5 ± 6.0 [cd]	321.4 ± 6.5 [ab]	3.74–5.66[b]
Tilia tomentosa	25.6 ± 1.7 [cd]	209.3 ± 5.6 [b]	4.26–5.09[b]

Different letters indicate significant difference among species (Tukey's post-hoc tests, $p < 0.05$)
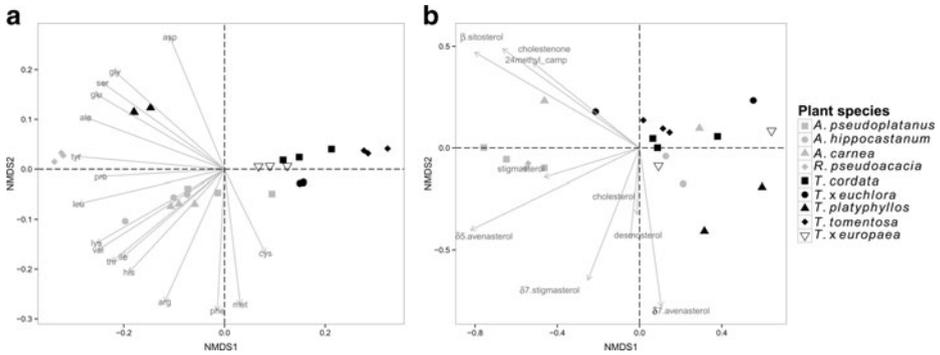
Fig. 2 Pollen composition in the studied tree species. nMDS ordination plot based on Bray-Curtis distances calculated on absolute amounts (µg/mg) of essential amino acids (a) and phytosterols (b). Ala, alanine; arg, arginine; asp, aspartic acid; cys, cysteine; glu, glutamic acid; gly, glycine; his, histidine; ile, isoleucine; leu, leucine; lys, lysine; met, methionine; phe, phenylalanine; pro, proline; ser, serine; thr, threonine; tyr, tyrosine; val, valine; 24methyl_camp, à 24-methylenecholesterol + campesterol

7 µg/mg) compared to *Acer pseudoplatanus* and *Robinia pseudoacacia* (> 9 µg/mg, $F_{8,12} = 5.315$, $p = 0.00512$; Table 1). Multivariate analyses detected significant differences in sterolic composition among all the studied tree species (perMANOVA, $F_{8,12} = 4.18$, $p = 0.001$). All species contained the same main sterols, i.e. β-sitosterol (> 33 % of total phytosterol) and δ5-avenasterol (> 15 % of total phytosterol) (Online Resource 2). However, pollen of *Tilia* species had lower concentrations in these phytosterols than the pollen of the other species ($\chi^2 = 87$, df = 8, $p = 0.003$ and $\chi^2 = 98$, df = 8, $p < 0.001$, respectively). Furthermore, pollen of *T. platyphyllos*, and to a lesser extent *T. x europaea* pollen, also contained a relatively high amount of δ7-avenasterol (approximately 30 % and 13 % of total phytosterols, respectively; Online Resource 2).

The quantity and chemical composition of nectar

The volume of nectar differed significantly among species; *Tilia* species (*T. cordata*, *T. x euchlora* and *T. tomentosa*) produced the highest quantities per flower compared with the other tree species (0.82–1.76 µl per flower, $\chi^2 = 62.73$, df = 8, $p < 0.001$; Fig. 3a). Sugar concentration varied between approximately 20 % for *Aesculus* species to 66 % for *Robinia pseudoacacia*. In consequence, sugar content per flower ranged from 0.16–0.28 mg in *Aesculus* species to 1.28 mg in *Robinia pseudiacacia*. Flower nectar from *Tilia* species presented sugar content comprised between 0.35 mg (*T. platyphyllos*) and 0.96 mg per flower (*T. x euchlora*). Nectar sugar content in *Acer pseudoplatanus* was about 0.67 mg per flower. Moreover, all *Tilia* nectars contained higher hexose (glucose + fructose) concentrations than the other species (Fig. 3b). Despite the variation in hexose and sucrose concentrations, all investigated species produced sucrose-rich nectar.

Discussion

Floral resource composition

To our knowledge, pollen composition is still rarely assessed for entomophilous plant species and was never tempted for street trees. We found that the pollen of the studied trees differed in
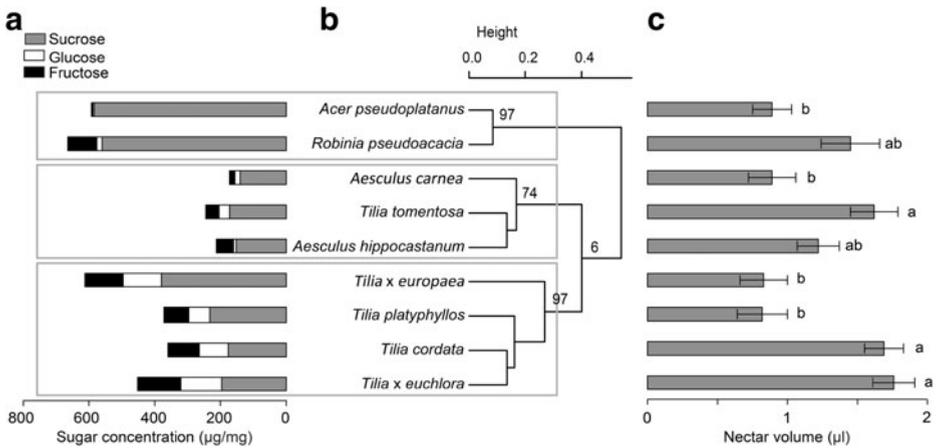
Fig. 3 Nectar volume and composition for the studied tree species. **a** Nectar sugar composition (concentration of fructose, glucose, and sucrose); **b** UPGMA cluster using Bray-Curtis dissimilarity index based on nectar sugar composition; **c** nectar volume per flower (μl; mean ± SD). The values near nodes are multiscale bootstrap resampling

composition. The polypeptide and total amino acid content of pollen varied widely among tree species and within genera. Similar differences among species have been previously reported. Among the nine studied species, *Tilia* species showed the lowest pollen quality as expressed in terms of amino acid and polypeptide concentrations. Weiner et al. (2010) also reported lower amino acid content in *Tilia* species (*T. cordata*) compared to *Acer* species (*A. platanoides*). However, the nine urban trees could be important protein resources for insects. A high nitrogen content in pollen, particularly when the total protein content is more than 20 %, is positively correlated with the development of bee larvae (Génissel et al. 2002; Tasei and Aupinel 2008; Vanderplanck et al. 2014b). All pollen of our investigated species contained more than 20 % total amino acids and all essential amino acids, which confirms their potential utility as pollen source. Furthermore, because urban trees provide pollen with a balanced amino acid content, they are likely to be attractive to pollen-collecting insects (Hanley et al. 2008; Weiner et al. 2010; Somme et al. 2015). Pollen of urban trees also could be sources of phytosterols for insect visitors. Bumble bees collect pollen that is high in both essential amino acids and sterols (Vaudo et al. 2015). Phytosterol concentration was particularly high in *Acer pseudoplatanus* and *Robinia pseudoplatanus* pollen. The main phytosterols found in pollen of urban trees (β-sitosterol and δ5-avenasterol) appear to be positively associated to larval development of bees (Vanderplanck et al. 2014b). However; pollen of *Tilia platyphyllos* and *T.* x *europaea* were also rich in δ7-avenasterol. This δ7-phytosterol is detrimental to herbivorous insects that lack the enzymes (specifically isomerases) necessary to convert δ7-sterols to δ5-sterols (Janson et al. 2009; Sedivy et al. 2011). Overall, the investigated plant species produced high quality pollen regarding amino acid and phytosterol composition although *Tilia* pollen seemed less interesting compared to the other urban trees.

Urban tree flowers provide nectar with relatively high sugar contents (0.16 to 1.28 mg/flower). The volume and sugar concentration of the produced nectar fell within the range of other bee-pollinated tree species (Percival 1961; Waser and Ollerton 2006) and was similar to those reported in previous studies (*T. cordata* and *T. platyphyllos*, Anderson 1976; *Aesculus*, Burke et al. 2000). Our results showed that the nectar sugar content varied widely within genera. For instance, the total sugar content of the nectar from the *Tilia* species ranged from

0.35 mg/flower to 0.96 mg/flower. Within the *Aesculus* species, *A. carnea* and *A. hippocastanum* produced nectar with similar sugar concentration but the values were much lower than those for two bee-pollinated North American congeners *A. glabra* (54 %; Macior 1978) and *A. sylvatica* (50 %; Burke et al. 2000). All nectar samples were sucrose-rich or -dominant, as previously reported (*A. pseudoplatanus*, *A. carnea*, *A. hippocastanum*, Percival 1961; *R. pseudoacacia*, *T.* x *europaea*, Wykes 1952; *T. cordata*, Käpylä 1978). Nectar that is sucrose-rich is highly attractive to honey bees and bumble bees (Percival 1961). The nectar of the studied species could thus be a valuable energy source for insects.

Even though nectar of urban trees was interesting regarding the sugar content, other compounds more detrimental for insects could be observed in nectar of some species. Bee deaths have been reported for *Tilia cordata*, *T. tomentosa* (Crane 1977; Pawlikoswski 2010), *T.* x *euchlora* (Pigott 2012) and *Aesculus hippocastanum* (Detzel and Wink 1993). Crane (1977) attributed these deaths to the presence in nectar of the sugar mannose, but Krasenbrink et al. (1994) failed to find mannose in *Tilia* nectar. Another explanation could be the presence of nicotine in lime nectar (Singaravelan et al. 2006; Naef et al. 2004). Mannose was not quantified in this study and evaluation of the toxicity of *Tilia* and *Aesculus* nectar need further investigations.

Floral resource availability

Wild insect populations are declining in human altered landscapes likely due to reduced availability of food resources (Potts et al. 2010a). In cities, gardens have been considered as abundant floral resources (Matteson and Langellotto 2010; Kaluza et al. 2016). Their steady food availability was most likely due to a mix of native and exotic plants which produce a continuous supply of resources, known to benefit generalist insect species (Harmon-Threatt and Kremen 2015; Baldock et al. 2015). Nevertheless, floral abundance has been reported to be a major limiting factor for the diversity of pollinating insects in urban gardens (Comba et al. 1999b; Frankie et al. 2005; Banaszak-Cibicka and Żmihorski 2012). Because a single tree produces thousands of flowers, the role of trees in sustaining populations of pollinating insects should be further considered. Even if herbaceous species might offer abundant pollen and nectar resources (Comba et al. 1999b; Baude et al. 2016), the flower density per square meter is lower than trees. The precise estimation of flower numbers remains difficult for trees as numbers depend on multiple variables like tree species, size, age, cutting practices, abiotic conditions (soil, climate), etc. Nevertheless, the mean flower density was estimated between 2400 flowers/m^2 for *Tilia* x *europaea* (D. Hicks, pers. comm.) to 4555 flowers/m^2 for *Acer pseudoplatanus* (Baude et al. 2016). In consequence, sugar nectar production of a *Tilia* x *europaea* tree could be more than 10 times the peak nectar sugar production of an equivalent patch of 'urban pollinator meadow' (D. Hicks, pers. comm.). Precise quantification of pollen production at the tree level will need further investigation.

Moreover, all studied tree species flower during the time of highest nectar and pollen demand for social insects like bumble bees (Dicks et al. 2015) and their flowering last from the begin of spring until end of August (Fig. 1). The first flowering urban trees are maple species (several species of *Acer*) that bloom as early as in April. They could therefore constitute a valuable resource at the stage of colony foundation for social insects (Moquet et al. 2015). According to our results, *Acer pseudoplatanus* was one of the most valuable pollen resource and its nectar production was intermediate compared to the other studied species. After the spring flowering species (*Aesculus*, *Robinia* …), *Tilia* species could be crucial resources at the maximum colony development stage in June and July. Although their pollen quality was lower

compared to the other investigated urban trees, they could be important protein and phytosterol resources for insects. Pollen is a limited plant resource and is, unlike nectar, not constantly replenished by the plant and can thus be depleted over the course of a day. Insects should thus primarily collect pollen when available. The effect of mass flowering species on a colony's pollen intake has been shown for several trees (Kaluza et al. 2016). In this perspective, urban trees might be valuable floral resource supply if their global production remains high all over the season. In consequence, future city planning needs to mix tree species along streets or inside a district.

Conclusion: Urban trees for increasing and diversifying floral resources for insects

Urban street trees could help to reduce disparities in time of floral resource abundance, type and diversity. As shown in this study, planting exotic trees (e.g. *Aesculus* spp., *R. pseudoacacia* or some *Tilia* species) could provide more opportunities for insects to find suitable floral resources. Currently only four native tree species, *A. pseudoplatanus*, *Tilia cordata*, *T. platyphyllos* and their hybrid *T.* x *europaea*, are generally planted as urban trees in European cities. It has recently been shown that if an exotic plant species can supply the necessary nutrients (i.e. pollen and/or nectar in quantity and quality), pollinating insects may readily incorporate them into their diets (Harmon-Threatt and Kremen 2015). Furthermore, expanding the diversity of the floral resources available for insects might allow generalist insects to mix pollen to complement or mitigate unfavourable pollen properties (i.e. pollen containing δ7-sterols; Eckhardt et al. 2014).

To offer nutritionally balanced resources for pollinating insects and to ensure flower availability during the season, it could be suggested planting different entomophilous trees along the streets in future city development projects. Despite this opportunity, other aspects regarding amenity trees, such as herbivores, pathogens or toxicity, need to be taken into account in urban design.

References

Acar C, Acar H, Eroğlu E (2007) Evaluation of ornamental plant resources to urban biodiversity and cultural changing: A case study of residential landscapes in Trabzon city (Turkey). Build Environ 42:218–229

Ahrné K, Bengtsson J, Elmqvist T (2009) Bumble bees (*Bombus* spp) along a gradient of increasing urbanization. PLoS One 4:e5574

Alton K, Ratnieks F (2013) To bee or not to bee. Biologist 60:12–15

Anderson GJ (1976) The pollination biology of *Tilia*. Am J Bot 63:1203–1212

Baldock KCR, Goddard MA, Hicks DM, et al. (2015) Where is the UK's pollinator biodiversity? the importance of urban areas for flower-visiting insects. Proc R Soc London B: Biol Sci 282:2014–2849

Banaszak-Cibicka W, Żmihorski M (2012) Wild bees along an urban gradient: winners and losers. J Insect Conserv 16:331–343

Bates AJ, Sadler JP, Fairbrass AJ, Falk SJ, Hale JD, Matthews TJ (2011) Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. PLoS One 6:e23459

Batra SWT (1985) Red maple (*Acer rubrum* L.), an important early spring food resource for honey bees and other insects. J Kansas Entomol Soc 58:169–172

Baude M, Kunin WE, Boatman ND, Conyers S, Davies N, Gillespie MA, Morton RD, Smart SM, Memmott JL (2016) Historical nectar assessment reveals the fall and rise of floral resources in Britain. Nature 530:85–88. doi:10.1038/nature16532

Bruxelles Environnement (2003) Rapport de synthèse sur l'état de l'environnement en Région de Bruxelles-Capitale - Edition 2002, Bruxelles

Burke JM, Wyatt R, dePamphilis CW, Arnold ML (2000) Nectar characteristics of interspecific hybrids and their parents in *Aesculus* (Hippocastanaceae) and *Iris* (Iridaceae). J Torrey Bot Soc 127:200–206

Cawoy V, Jonard M, Mayer C, Jacquemart A-L (2012) Do abundance and proximity of the alien *Impatiens glandulifera* affect pollination and reproductive success of two sympatric co-flowering native species? J Poll Ecol 10:130–139

Cierjacks A, Kowarik I, Joshi J, Hempel S, Ristow M, von der Lippe M, Weber E (2013) Biological flora of the British Isles: *Robinia pseudoacacia*. J Ecol 101:1623–1640

Cnaani J, Thomson JD, Papaj DR (2006) Flower choice and learning in foraging bumblebees: effects of variation in nectar volume and concentration. Ethology 112:278–285

Collins J, Kinzig A, Grimm N, Fagan W, Hope D, Wu J, Borer E (2000) A new urban ecology. Am Sci 88:416–425

Comba L, Corbet SA, Barron A, Bird A, Collinge S, Miyazaki N, Powell M (1999a) Garden flowers: insect visits and the floral reward of horticulturally-modified variants. Ann Bot 83:73–86

Comba L, Corbet SA, Hunt L, Warren B (1999b) Flowers, nectar and insect visits: evaluating British plant species for pollinator-friendly gardens. Ann Bot 83:369–383

Corbet SA (2003) Nectar sugar content: estimating standing crop and secretion rate in the field. Apidologie 34:1–10

Corbet SA, Bee J, Dasmahapatra K, Gale S, Gorringe E, La Ferla B, Moorhouse T, Trevail A, Van Bergen Y, Vorontsova M (2001) Native or exotic? Double or single? evaluating plants for pollinator-friendly gardens. Ann Bot 87:219–232

Couvillon MJ, Schürch R, Ratnieks FLW (2014) Waggle dance distances as integrative indicators of seasonal foraging challenges. PLoS One 9:e93495

Crane E (1977) Dead bees under lime trees. Bee World 58:129–130

Dafni A, Kevan PG, Husband BC (eds) (2005) Practical pollination biology. Enviroquest, Cambridge, Ontario, Canada

Detzel A, Wink M (1993) Attraction, deterrence or intoxication of bees (*Apis mellifera*) by plant allelochemicals. Chemoecology 4:8–18

Dicks LV, Baude M, Roberts SPM, Phillips J, Green M, Carvell C (2015) How much flower-rich habitat is enough for wild pollinators? Answering a key policy question with incomplete knowledge. Ecol Entomol 40:22–35

Eckhardt M, Haider M, Dorn S, Müller A (2014) Pollen mixing in pollen generalist solitary bees: a possible strategy to complement or mitigate unfavourable pollen properties? J Anim Ecol 83:588–597

Everaars J, Strohbach MW, Gruber B, Dormann CF (2011) Microsite conditions dominate habitat selection of the red mason bee (*Osmia bicornis*, Hymenoptera: Megachilidae) in an urban environment: A case study from Leipzig, Germany. Landsc Urban Plan 103:15–23

Frankie GW, Thorp RW, Schindler M, Hernandez J, Ertter B, Rizzardi M (2005) Ecological patterns of bees and their host ornamental flowers in two Northern California cities. J Kansas Entomol Soc 78:227–246

Garbuzov M, Ratnieks FLW (2014) Quantifying variation among garden plants in attractiveness to bees and other flower-visiting insects. Funct Ecol 28:364–374

Génissel A, Aupinel P, Bressac C, Tasei JN, Chevrier C (2002) Influence of pollen origin on performance of *Bombus terrestris* micro-colonies. Entomol Exper Applic 104:329–336

Gonzalez-Teuber M, Heil M (2009) Nectar chemistry is tailored for both attraction of mutualists and protection from exploiters. Pl Signal Behav 4:809–813

Goslee SC, Urban DL (2007) The ecodist package for dissimilarity-based analysis of ecological data. J Stat Softw 22:1–19

Goulson D (2009) Bumble bees: behaviour, ecology, and conservation, 2nd edn. Oxford University Press, USA

Goulson D, Darvill B (2004) Niche overlap and diet breadth in bumblebees. are rare species more specialized in their choice of flowers? Apidologie 35:55–63

Goulson D, Hughes W, Derwent L, Stout J (2002) Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. Oecologia 130:267–273

Goulson D, Sparrow KR (2008) Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. J Insect Conserv 13:177–181

Gunnarsson B, Federsel LM (2014) Bumble bees in the city: abundance, species richness and diversity in two urban habitats. J Insect Conserv 18:1185–1191

Haaland C, Gyllin M (2010) Butterflies and bumblebees in greenways and sown wildflower strips in Southern Sweden. J Insect Conserv 14:125–132

Hanley ME, Awbi AJ, Franco M (2014) Going native? flower use by bumblebees in English urban gardens. Ann Bot 113:799–806

Hanley ME, Franco M, Pichon S, Darvill B, Goulson D (2008) Breeding system, pollinator choice and variation in pollen quality in British herbaceous plants. Funct Ecol 22:592–598

Harmon-Threatt AN, Kremen C (2015) Bumble bees selectively use native and exotic species to maintain nutritional intake across highly variable and invaded local floral resource pools. Ecol Entomol 40: 471–478

Hernandez J, Frankie G, Thorp R (2009) Ecology of urban bees: a review of current knowledge and directions for future study. Cities and the Environment 2:2–15

Hunter MR, Hunter MD (2008) Designing for conservation of insects in the built environment. Insect Conserv Div 1:189–196

Janson EM, Grebenok RJ, Behmer ST, Abbot P (2009) Same host-plant, different sterols: variation in sterol metabolism in an insect herbivore community. J Chem Ecol 35:1309–1319

Kaluza BF, Wallace H, Heard TA, Klein AM, Leonhardt SD (2016) Urban gardens promote bee foraging over natural habitats and plantations. Ecol Evol 6:1304–1316

Käpylä M (1978) Amount and type of nectar sugar in some wild flowers in Finland. Ann Bot Fenn 15:85–88

Kevan PG (1990) How large bees, *Bombus* and *Xylocopa* (Apoidea Hymenoptera) forage on trees: optimality and patterns of movement in temperate and tropical climates. Ethol Ecol Evol 2:233–242

Kitaoka TK, Nieh JC (2009) Bumble bee pollen foraging regulation: role of pollen quality, storage levels, and odor. Behav Ecol Sociobiol 63:625–625

Krasenbrink A, Popp M, Denker B (1994) Nektarzusammensetzung von *Tilia tomentosa* (Moench) und anderen Lindenarten/−hybriden. Z. Okologie und Naturschutz 3:237–242

Lambinon J, Verloove F (2012) Nouvelle Flore de Belgique, du Grand-Duché de Luxembourg, du Nord de la France et des régions voisines, 6th edn. Meise, Belgium

Macior LW (1978) Pollination ecology of vernal Angiosperms. Oikos 30:452–460

Matteson KC, Langellotto GA (2010) Determinates of inner city butterfly and bee species richness. Urban Ecosyst 13:333–347

McFrederick QS, Le Buhn G (2006) Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)? Biol Conserv 129:372–382

McKinney ML (2008) Effects of urbanization on species richness: A review of plants and animals. Urban Ecosyst 11:161–176

Moquet L, Mayer C, Michez D, Wathelet B, Jacquemart AL (2015) Early spring floral foraging resources for pollinators in wet heathlands in Belgium. J Insect Conserv 19:837–848

Naef R, Jaquier A, Velluz A, Bachofen B (2004) Fron the linden flower to linden honey - volatile constituents of linden nectar, and extract of bee-stomach and ripe honey. Chem Biodivers 1:1870–1879

Nicolson SW (2011) Bee food: the chemistry and nutritional value of nectar, pollen and mixtures of the two. Afr Zool 46:197–204

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H (2013). Vegan: community ecology package. R package version 2.0–9.http://CRAN. R-project.org/package=vegan. Accessed: 2014 July 20

Pauleit S, Jones N, Garcia-Martin G, Garcia-Valdecantos JL, Rivière LM, Vidal-Beaudet L, Bodson M, Randrup T (2002) Tree establishment practice in towns and cities – results from a European survey. Urban For Urban Green 1:83–96

Pawelek J, Frankie G, Thorp R, Przybylski M (2009) Modification of a community garden to attract native bee pollinators in urban San Luis Obispo, California. Cities and the Environment 2:7–21

Pawlikowski T (2010) Pollination activity of bees (Apoidea: Apiformes) visiting the flowers of *Tilia cordata* Mill. and *Tilia tomentosa* Moench in an urban environment. J Apic Sci 54:73–79

Percival MS (1961) Types of nectar in Angiosperms. New Phytol 60:235–281

Pigott C (2012) Lime-trees and basswoods: a biological monograph of the genus *Tilia*. Cambridge Univ Press, Cambridge, UK

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010a) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25:345–353

Potts SG, Roberts S, Dean R, Morris G, Brown M, Jones R, Neumann P, Settele J (2010b) Declines of managed honey bees and beekeepers in Europe. J Apic Res 49:134–136

R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org

Roulston TH, Cane JH (2000) Pollen nutritional content and digestibility for animals. Plant Syst Evol 222:187–209

Salisbury A, Armitage J, Bostock H, Perry J, Tatchell M, Thompson K (2015) Enhancing gardens as habitats for flower-visiting aerial insects (pollinators): should we plant native or exotic species? J Appl Ecol 52:1156–1164

Sedivy C, Müller A, Dorn S (2011) Closely related pollen generalist bees differ in their ability to develop on the same pollen diet: evidence for physiological adaptations to digest pollen. Funct Ecol 25:718–725

Singaravelan N, Inbar M, Ne'eman G, Distl M, Wink M (2006) The effects of nectar-nicotine on colony fitness of caged honeybees. J Chem Ecol 32:49–59

Sirohi MH, Jackson J, Edwards M, Ollerton J (2015) Diversity and abundance of solitary and primitively eusocial bees in an urban centre: a case study from Northampton (England). J Insect Conserv 19:487–500

Sjöman H, Gunnarsson A, Pauleit S, Bothmer R (2012a) Selection approach of urban trees for inner-city environments: learning from nature. Arboricult Urban For 38:194–204

Sjöman H, Östberg J, Bühler O (2012b) Diversity and distribution of the urban tree population in ten major Nordic cities. Urban For Urban Green 11:31–39

Somme L, Vanderplanck M, Michez D, Lombaerde I, Moerman R, Wathelet B, Wattiez R, Lognay G, Jacquemart AL (2015) Pollen and nectar quality drive the major and minor floral choices of bumble bees. Apidologie 46:92–106

Suzuki R, Shimodaira H (2006) Pvclust: an R package for assessing the uncertainty in hierarchical clustering. Bioinformatics 22:1540–1542

Tasei JN, Aupinel P (2008) Nutritive value of 15 single pollens and pollen mixes tested on larvae produced by bumble bee workers (Bombus terrestris, Hymenoptera: Apidae). Apidologie 39:397–409

Tedeschini E, Rodriguez-Rajo FJ, Caramiello R, Jato V, Frenguelli G (2006) The influence of climate changes in Platanus spp. pollination in Spain and Italy. Grana 45:222–229

Thomson D (2004) Competitive interactions between the invasive European honey bee and native bumble bees. Ecology 85:458–470

Vanderplanck M, Leroy B, Wathelet B, Wattiez R, Michez D (2014a) Standardized protocol to evaluate pollen polypeptides as bee food source. Apidologie 45:192–204

Vanderplanck M, Michez D, Vancraenenbroeck S, Lognay G (2011) Micro-quantitative method for analysis of sterol levels in honeybees and their pollen loads. Anal Lett 44:1807–1820

Vanderplanck M, Moerman R, Rasmont P, Lognay G, Wathelet B, Wattiez R, Michez D (2014b) How does pollen chemistry impact development and feeding behaviour of polylectic bees? PLoS One 9:e86209

Vaudo AD, Tooker JF, Grozinger CM, Patch HM (2015) Bee nutrition and floral resource restoration. Curr Opin Insect Sci 10:133–141

Vervoort A, Cawoy V, Jacquemart AL (2011) Comparative reproductive biology in co-occurring invasive and native Impatiens species. Int J Plant Sci 172:366–377

Villette C, Berna A, Compagnon V, Schaller H (2015) Plant sterol diversity in pollen from Angiosperms. Lipids 50:749–760

Waser NM, Ollerton J (2006) Plant-pollinator interactions: from specialization to generalization. University of Chicago Press, Chicago, USA

Weiner CN, Hilpert A, Werner M, Linsenmair KE, Blüthgen N (2010) Pollen amino acids and flower specialisation in solitary bees. Apidologie 41:476–487

Weryszko-Chmielewska E, Tietze M, Michońska M (2012) Ecological features of the flowers of Aesculus hippocastanum L. and characteristics of Aesculus L. pollen seasons under the conditions of Central-Eastern Poland. Acta Agrobot 65:61–68

Williams IH, Carreck N, Little DJ (1993) Nectar sources for honey bees and the movement of honey bee colonies for crop pollination and honey production in England. Bee World 74:160–175

Winfree R, Aguilar R, Vázquez DP, Le Buhn G, Aizen MA (2009) A Meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90:2068–2076

Wojcik VA, Frankie GW, Thorp RW, Hernandez JL (2008) Seasonality in bees and their floral resource plants at a constructed urban bee habitat in Berkeley, California. J Kansas Entomol Soc 81:15–28

Wykes GR (1952) An investigation of the sugars present in the nectar of flowers of various species. New Phytol 51:210–215