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The nectar report: Quantitative review of nectar sugar concentrations offered by bee visited flowers in agricultural and non-agricultural landscapes

Tobias Pamminger Corresp., 1, Roland Becker 1, Sophie Himmelreich 1, Christof W Schneider 1, Matthias Bergtold 1

1 Global Ecotoxicology, BASF SE, Limburgerhof, Germany

Corresponding Author: Tobias Pamminger
Email address: tobias.pamminger@basf.com

There is growing concern that some bee populations are in decline potentially threatening pollination security in agricultural and non-agricultural landscapes. Among the numerous causes associated with this trend nutritional stress, resulting from a mismatch between bee nutritional needs and plant community provisioning, has been suggested as one potential driver. To ease nutritional stress on bee populations in agricultural habitats, agri-environmental protection schemes aim to provide alternative nutritional resources for bee populations during times of need. However, such efforts have focused mainly on quantity (providing flowering plants) and timing (flower-scarce periods), while largely ignoring the quality of the offered flower resources. In a first step to start addressing this information gap we have compiled a comprehensive geographically explicit dataset on nectar quality (i.e. total sugar concentration), offered to bees both within fields (crop and weed species) as well as off field (wild) around the globe. We find that the total nectar sugar concentrations in general do not differ between the three plant communities studied. In contrast we find increased quality variability in the wild plant community compared to crop and weed community, which is likely explained by the increased phylogenetic diversity in this category of plants. In a second step we explore the influence of local habitat on nectar quality and its variability utilizing a detailed sunflower (Helianthus annuus L.) data set and find that geography has a small, but significant influence on these parameters. In a third step we identify crop groups (genera), which provide sub-optimal nectar resources for bees and suggest high quality alternatives as potential nectar supplements. In the long term this data base could serve as a starting point to systematically collect more quality characteristics of plant provided resources to bees, which ultimately can be utilized by scientist, regulators, NGOs and farmers to improve the flower resources offered to bees. We hope that ultimately this data will help to ease nutritional stress for bee populations and foster a data informed discussion about pollinator conservation in modern agricultural
landscapes.
The nectar report: Quantitative review of nectar sugar concentrations offered by bee visited flowers in agricultural and non-agricultural landscapes

Pamminger T*, Becker R¹, Himmelreich S¹, Schneider CW¹ & Bergtold M¹

¹ BASF SE, Speyererstr. 2, 67117 Limburgerhof, Germany,

* Corresponding author
E-mail: tobias.pamminger@basf.com

Abstract

There is growing concern that some bee populations are in decline potentially threatening pollination security in agricultural and non-agricultural landscapes. Among the numerous causes associated with this trend nutritional stress, resulting from a mismatch between bee nutritional needs and plant community provisioning, has been suggested as one potential driver. To ease nutritional stress on bee populations in agricultural habitats, agri-environmental protection schemes aim to provide alternative nutritional resources for bee populations during times of need. However, such efforts have focused mainly on quantity (providing flowering plants) and timing (flower-scarce periods), while largely ignoring the quality of the offered flower resources. In a first step to start addressing this information gap we have compiled a comprehensive geographically explicit dataset on nectar quality (i.e. total sugar concentration), offered to bees both within fields (crop and weed species) as well as off field (wild) around the globe. We find that the total nectar sugar concentrations in general do not differ between the three plant communities studied. In contrast we find increased quality variability in the wild plant community compared to crop and weed community, which is likely explained by the increased phylogenetic diversity in this category of plants. In a second step we explore the influence of local habitat on nectar quality and its variability utilizing a detailed sunflower (*Helianthus annuus* L.) data set and find that geography has a small, but significant influence on these parameters. In a third
step we identify crop groups (genera), which provide sub-optimal nectar resources for bees and suggest high quality alternatives as potential nectar supplements. In the long term this data base could serve as a starting point to systematically collect more quality characteristics of plant provided resources to bees, which ultimately can be utilized by scientist, regulators, NGOs and farmers to improve the flower resources offered to bees. We hope that ultimately this data will help to ease nutritional stress for bee populations and foster a data informed discussion about pollinator conservation in modern agricultural landscapes.

Introduction

Pollinators are an integral part of natural as well as agricultural ecosystems, with the majority of flowering plants relying on their ecosystem services (Ollerton, Winfree et al. 2011). Over the past decades bee pollinators have received particular attention, following the realization that some populations seem to decline (Biesmeijer, Roberts et al. 2006, Potts, Biesmeijer et al. 2010, Ollerton, Erenler et al. 2014). While managed honey bee populations appear to suffer only in restricted geographic regions and in some years (Moritz and Erler 2016), the focus of concern has recently extended to wild bees (Roulston and Goodell 2011, Goulson, Nicholls et al. 2015, Vaudo, Tooker et al. 2015). Numerous potential drivers for this proposed dynamic have been put forward including changes in land use, agricultural intensification, habitat loss- or fragmentation, emerging pathogens and their interactions (Brown and Paxton 2009, Winfree, Aguilar et al. 2009, Goulson, Nicholls et al. 2015). While all these factors likely contribute to some degree, changes in flower provided food resource for bees has emerged as prime candidate directly regulating bee populations (Roulston and Goodell 2011). Bees and their larvae almost exclusively rely on flower derived nutrients, namely nectar as their primary source of carbohydrates and pollen for protein, lipids, and other micronutrients essential for development, health and survival (Michener 2000, Brodschneider and Crailsheim 2010, Roulston and Goodell 2011). Large scale changes in land-use can alter the quality, abundance and availability of relevant flower derived resources, which in turn can result in nutritional mismatch leading to nutritional stress for bee populations with potential
adverse effects (Potts, Biesmeijer et al. 2010, Roulston and Goodell 2011, Goulson, Nicholls et al. 2015). For example, while bee pollinated crops might provide a cornucopia of flower derived resources during their discreet flowering period, the lack of alternative food sources in monocultural dominated agricultural settings, might put a strain on bee species foraging outside the flowering period.

In order to ease nutritional stress on bee populations in agricultural settings the establishment of selective foraging habitats has been incentivized via agro-environmental management schemes in the EU and elsewhere (Phillips and Lowe 2005, Vaughan and Skinner 2008, Lye, Park et al. 2009, Goulson, Nicholls et al. 2015, Potts, Biesmeijer et al. 2015). Such schemes seek to provide bees with alternative complementary flower resources outside the mass flowering periods of commercial crops, but have traditionally focused solely on providing plants to attract and sustain a diverse bee community (Vaudo, Tooker et al. 2015). However, quantity and timing alone are likely insufficient to maintain healthy bee populations (Vaudo, Tooker et al. 2015). The quality of floral resources (e.g. sugar content of nectar) also plays a major role in bee health with direct consequences for bee’s fitness (Brodschneider and Crailsheim 2010, Vaudo, Tooker et al. 2015, Vaudo, Patch et al. 2016). Such qualitative aspects of bees nutrition should be taken into consideration to develop a complementary and nutritionally optimized resource base for bee populations in agricultural landscapes in order to improve the nutritional basis for bee populations in agricultural environments (Vaudo, Tooker et al. 2015).

As a first step to facilitate the integration of flower resource quality in pollinator management we have compiled a geographically explicit data base of nectar quality (measured as total sugar concentration) provided by bee visited flowers in an agricultural setting. Given that nectar is the main carbohydrate source for adults as well as developing bees sugar concentration is directly linked to the amount of sugar bees can extract from flowers and has traditionally served as a proxy for nectar quality (Roulston and Goodell 2011, Vaudo, Tooker et al. 2015). We use this data base to compare the quality and quality variability of nectar resource bees can encounter in agricultural landscapes in- (crop and weeds) and off-field (wild) around the globe. In a second step we utilize a unique historical data set to analyze the influence of local habitat and water stress on nectar
sugar concentrations and their variability. In a last step we identify crop genera, which provide sub-optimal nectar quality and suggest plant groups which could serve as high quality alternatives during times of need.

Materials and Methods

Data collection and categorization

In late 2017 and early 2018 we searched the literature for records on nectar quality in bee pollinated flowers using ISI web of knowledge and google scholar as main information sources. We used alterations of the search terms: “bee”, “pollinator”, “nectar” and “sugar concentration” to identify the relevant publications and extended our search to literature cited within them. In addition, we extended our data gathering efforts to the French and German literature to provide a more complete picture and make this information easier accessible to the English speaking scientific community.

Plant selection

Plant species were categorized as bee visited if either bee pollination was directly observed or the flowers were explicitly classified as “melittophil” based on their floral characteristics by the study authors. In addition, we used the USDA pollinator manual (McGregor 1976) and the expertise of BASF plant experts for cross validation of the derived classifications.

Geographic localization

We chose to map the plant distribution on a continental scale because this information was available for the majority of plant species included in the data set. We decided to choose the Panama Canal as separation line between North and South America the Ural and the black sea to separate Europe from Asia and the Suez Canal to separate Asia and Africa. Using the encyclopedia of life (http://eol.org/) as main source for plant distribution we recorded the presence and absence of collection records of each plant species on the five continents. This very broad geographical classification is intended as a first attempt to make this information geographically explicit and should serve as a starting point to
add more detailed information on the local geographic (e.g. national or region) or habitat characteristics in the future. Such information will be vital to make more precise predictions about the temporal quality dynamics in agricultural landscapes around the globe.

Categorization of crop, weed and wild plants
The selected plants were categorized as crop species if they were listed as “cultivated crops” in governmental data bases (e.g. USDA: https://plants.usda.gov and European commission plant variety catalogue: https://ec.europa.eu, (McGregor 1976)), the open primary literature or were known as such to our BASF crop experts. All remaining plants without such records were categorized as non-cultivated. In a second step these non-cultivated plants were categorized either as a weed species, in case they were listed in an agricultural or governmental weed data resource (e.g. USA Noxious weed data base https://plants.usda.gov, Australia weeds http://www.environment.gov.au or industry compendium (Bayer 1992)), or as wild plants in case they were no such recorded were found. Once a plant species was categorized (as crop weed or wild) in one geographic region it was classified as such in all other regions where it was present.

Resource quality
We used sugar (total carbohydrate) concentration in nectar (% w/w) as proxy for nectar quality. This quality characteristic was chosen because it is the most frequently reported quantitative measurement of nectar quality in the literature, and is directly related to bee fitness (Vaudo, Tooker et al. 2015). However, it is important to mention that other quality criteria (e.g. sugar composition, nectar volume as well as the presence and absence of non-sugar compounds) are also important markers for resource quality (Vaudo, Tooker et al. 2015).

Nectar quality categorization
Nectar serves as the main carbohydrate source for bees and consequently the total caloric value as well as the rate of calorie uptake are important aspects of nectar quality for bees. One of the main factors determining uptake rate is nectar viscosity, which in turn is largely determined by nectar sugar concentration. Based on uptake measurements and theoretical consideration the bee optimal concentration range was determined as 35-65% (Kim, Gilet et al. 2011). While this is a theoretical optimal range and bees seem to prefer higher over lower nectar sugar concentrations (Wykes 1952, Roubik and Buchmann 1984, Cnaani, Thomson et al. 2006) they will collect nectar with sugar concentrations below that value under natural conditions (e.g. (Roubik and Buchmann 1984)). However, all evidence suggests that bees avoid foraging on nectar sources below 20% sugar concentration, likely because the caloric intake cannot support sustained foraging activity with potentially detrimental effects for the bee colony (Maurizio and Grafl 1980, Roubik and Buchmann 1984, Cnaani, Thomson et al. 2006). Based on these criteria we define nectar concentrations of 65-35% as optimal 35-20% as adequate and nectar sugar concentrations below 20% low quality.

Analysis

Nectar quality and its variability in bee visited plants

In the first part of the analysis we focused on the broad picture of nectar quality and its variation provided by a given plant community (crop, weeds and wild) on all relevant continents around the globe. In addition, we explore the possible of intrinsic differences in nectar quality variability of the plant species belonging to the different communities (crop, weed and wild) using plant species where we had multiple quality measurements (N>3) to calculate standard deviation (SD) as a proxy for within species variability.

The influence of local habitat on nectar quality and its variability

During our non-english literature screening we discovered a data set (Simidtschiev 1988), which is uniquely suited to isolate the contribution of geographic location and water availability to nectar sugar concentrations and its variation in the sunflower (Helianthus annuus L.). In order to make this data easier accessible to the scientific community, we
will give a brief summary of the materials and methods used. Between 1981 and 1986 a field experiment was conducted at two field sites in Bulgaria (Toshevo in north-east and Plovdiv in central Bulgaria) separated by more than 300 km. Over this time period 52 different sunflower variants and hybrids, originating from different geographical regions around the globe (including Europe, North America, South America and Australia), were grown under standard agronomical conditions at both locations in paired design. The nectar sugar concentration for all varieties were measured each year on 25 flowers per variant/hybrid day and location (200-300 measurements per year) using a capillary based extraction method and an Abbe Refractometer. In a second experiment, the author tested the effect of irrigation (watering vs. no watering) Using this unique data set (Simidtschiev 1988) we explore the influence of location on nectar sugar concentration variation in the sunflower taking advantage of the paired design of the study.

Nectar quality offered by plant genera

In a last step we compared the quality of crop genera in terms of nectar quality. We used all genera, where we had measurements for more than 3 plant species belonging to this genus. We categorized them according to our pre-defined (see above) as optimal (35-65%), adequate (34-20%) and low quality (below 20%). We used this information to identify crop genera offering low quality nectar and potential genera offering high nectar quality as potential replacements.

Statistics

Both statistical analysis and graphs generation were conducted in R v. 3.3.3. We used descriptive statistics, conservative non-parametric Kruskal-Wallis (KW) test and Bonferroni corrected pairwise Wilcoxon-test (paired or not paired) as post hoc test in cases where the KW test indicated significant difference between groups. In order to analyse homogeneity of variance in nectar concentration between groups we used the non-parametric Fligner-test and Bonferroni corrected pairwise Fligner-test in case the
main test indicated significant differences between groups as post hoc test. Significance level were set to $\alpha = 0.05$ in all cases.

Results

Data summary

In total we collected 322 individual measurements of sugar concentration in nectar for bee pollinated flowers ranging from 6.3 – 85%. With similar sampling sizes for plant species in crop (N = 151) and wild plants (N = 141), but fewer measurements for weeds (N=30). On a Genus level we find that the wild community has the highest phylogenetic diversity in terms of number of genera recorded (N = 63) followed by the crop community (N = 29) and the lest diversity in the weed community (N = 18). In general, the recorded data is evenly spread across the geographic regions (see Table 1), however only a limited number of weed species could be identified in Africa (N=13) and South America (N=18). The summary statistics including mean, median 10th and 25th Percentile are presented in Table 1.

Nectar quality & variability

Overall nectar concentration in all regions were comparable around a median value of 40% sugar concentration (see Figure 1, Tab.1) and no significant differences between crop, weed or wild plant communities were found globally (KW chi$^2$ = 3.2, p = 0.2) or within the different geographic regions (all KW chi$^2$ < 4.48, p > 0.11; see Figure 1 and Table 1).

In contrast to the median concentrations we find that the three plant communities differed in the variability of nectar quality (Global community; Fligner test chi$^2$ = 31.97, p < 0.001). This effect is mainly driven by an increased variability of the wild community (see Fig.1) which differs significantly from the crop community on a global level (Bonferroni corrected pairwise Fligner test crop x wild chi$^2$ = 30.64 , p < 0.001), with a similar trend in the same direction when compared to the weed community (Bonferroni corrected pairwise Fligner test; crop x weed chi$^2$ = 5.02 , p = 0.08). In contrast we find that crop and weed species clearly do not differ in terms of their variability (Bonferroni corrected pairwise Fligner test
weed x wild \chi^2 = 1.01, p = 0.93). When comparing the variability of nectar quality on a species level we find that we had only had a limited number of species where we had multiple nectar measurements (N > 2) recorded (crop N = 18, weed N = 6 and wild N = 18). Using this limited data set we find no indication of intrinsic differences in variability (measured as SD) of plant species belonging to the three different (KW \chi^2 = 2.52, p = 0.28).

The influence of local habitat on nectar quality and its variability

When reanalyzing the Simidtschiev (1988) sunflower dataset comparing nectar sugar concentrations we find that geographic location has a small (Median_{Toschevo} = 30.7\%, Median_{Plovdiv} = 36.05\% see Fig.2), but significant influence on nectar concentrations (paired Wilcoxon test: V = 216, p < 0.0001 see Fig.2) and its variation (Fligner test \chi^2 = 6.12, p = 0.01 see Fig.2). When looking at the effect of non-irrigation (natural rainfall) on nectar sugar concentration of the four tested sunflower varieties Simidtschiev's analysis (1988) finds that in three of the four verities watering did not significantly influence nectar sugar concentration and in the fourth cultivar (hybride 260) it only decreased it by about 3.4\% (mean irrigation = 50.3, mean natural rainfall = 53.7\%).

Nectar quality on a genus level

In total we recorded multiple measurements for 12 crop and 15 non-crop genera and find that there is a significant differences in nectar sugar concentration between them (KW \chi^2 = 100.68, p < 0.0001 Fig.3). When comparing the nectar quality according to our categorization (see above) our results indicate that two crop genera, namely Capsicum (including paprika and chili) and Pyrus (pear), offer low quality nectar (median sugar concentration < 20\%. (see Fig. 3). When looking at the genera offering high quality nectar we were able to identify 15 Genera which provide optimal nectar concentrations (35\%-65\%) for bees (see Fig.3).
Discussion

In this study we have compiled the first comprehensive data set on nectar quality provided by bee visited plants in agricultural landscapes around the globe. Our data indicates that nectar sugar concentrations in bee visited flowers is strongly conserved across all communities and geographic regions with a median value around 40% (see Fig. 1 and Tab.1). In addition, we find that wild plants exhibit stronger variation in nectar concentrations at the community level when compared to crop plants. However, this difference is not reflected on the species level. Using a comprehensive data set from the German literature (Simidtschiev 1988) on sunflower varieties we find evidence that microhabitat (e.g. water availability) and geographic region might have a more limited effect on nectar sugar concentration and its variation than previously thought. Using the complete data set we identify two crop genera (Capsicum and Pryrus) which provide low quality nectar to bees during their flowering period and suggest 15 possible genera which provide high quality nectar as potential supplement nectar source.

When looking at the recorded nectar sugar concentrations we find strong support for the well-established idea that flowers are under strong selection pressure to provide nectar suitable for their respective pollinators (Baker 1975, Harder 1986, Perret, Chautems et al. 2001). In the case of bees, the literature suggests optimal values ranging from 35-65% which is well supported by our data (Waller 1972, Harder 1986, Kim, Gilet et al. 2011). It has been suggested that the pollinator preferences for different sugar concentrations could be explained by different modes of nectar intake, which in case of bees favours higher viscosity and consequently sugar concentrations (Kim, Gilet et al. 2011). Our results therefore indicate that nectar quality between different plant communities in agricultural landscapes and their surroundings are 1) closely matched to pollinators needs 2) comparable between all regions and 3) in principal likely sufficient to maintain healthy bee pollinator populations.

In contrast to the median sugar concentrations we find elevated nectar quality variability of the wild plant community compared to the crop and likely weed plants communities (see Fig. 1). However, based on the results of our limited species level data
set we have no indication that this pattern is reflected on the species level where plants
of the different communities exhibited comparable variability. In particular the species
belonging to the weed community are interesting in this regard as they are wild species
which grow under (invade) standardized agricultural conditions. A priori we could expect
that the more standardized growing conditions in agricultural could reduce nectar quality
variability when compared to natural habitats. As we do not find differences between
these three groups on the species level our results support the view that growing
conditions might have a more limited influence on the variability of nectar sugar
concentration and supports a plant species specific nectar concentration of at least some
species. In turn this suggest that the observed variation on the community level likely
reflects the elevated phylogenetic diversity in wild plants compared to crop and weed
species (Meyer, DuVal et al. 2012). Indeed, when looking at the community level, we find
the wild community containing more than twice the number of wild genera (N=63)
compared to the crop (N=29), as well as the weed community (N=18), which seems the
most likely explanation for the observed pattern.

The comprehensive study of Simidtschiev (1988) offers the unique opportunity to
study the effects of geography and water availability on nectar sugar concentration. These
findings support our initial findings that geography, in this case only has a limited absolute
effect on nectar sugar concentration and its variation in ab (See Fig. 2). In particular the
fact that plants “defended” their nectar sugar concentrations against variation in water
availability suggest that at least sunflowers have plant species specific nectar sugar
concentrations. In his original analysis Simidtschiev (1988) suggests that instead of
changes in nectar concentration, nectar volume responds to reduced water availability,
which in turn reduce the caloric value and consequently resource quality for bees. It would
be interesting to analyse what parameters best explain the observed variation (including
temperature, rainfall soil types ect.) because such factor undoubtedly play a role in
shaping nectar concentrations to some degree (Corbet, Willmer et al. 1979).
Unfortunately, these parameters were not recorded by Simidtschiev (1988) for the study
duration. This highlights the importance of multiple measurements to adequately
characterize resource quality for bees. In a next step it would be very important to include
such measurements into the data base to provide a more detailed picture of nectar quality
to serve as a robust basis to improve the resource quality offered to bee populations in the future.

In our quality analysis we have identified two genera of crop plants, which provide low quality nectar sugar concentrations. While it is well-known that pears (Pyrus) are not considered attractive to bees due to their low nectar (Fig.3) quality (Maurizio and Grafl 1980) the even lower levels in Capsicum (e.g. paprika and chilies) suggest that these crop will likely not be able to sustain bee populations on their own and are likely avoided by bees if alternatives are present. Such information, coupled with detailed information regarding geographic abundance of these crops, could be used to identify potential targets for a resource quality intervention such as agro-environmental scheme. Our data suggest 15 genera which provide high quality alternatives which could be used as high-quality alternative. In particular orchards might be a good target for such measures as the targeted resource interventions could be located close to the orchard which in turn could retain bees, in particular wild bees, in the area and increase overall pollination.

Our study is a first step towards the integration of resource quality in bee conservation practices. The obvious next step could be to include additional quality markers for nectar including nectar volume, sugar composition and non-sugar components, which clearly play an important role in determining nectar quality for bees (Vaudo, Tooker et al. 2015). A second important step would be to compile a similar data set for the second important flower resource pollen and its quality markers such as crude protein content, amino acid composition, lipid content and the presence of potential adverse components. Such information should be combined with detailed geographic and information on exact flowering periods in order to estimate the resource availability and quality during the season in a given location and plan and implement targeted interventions to support bee populations.

Such a tool could support farmers, Scientists, Regulators NGOs and the industry when designing optimized alternative flower resources for bees in agricultural landscapes. We hope that this data set will serve as a starting point to help facilitate a data informed discussion about pollinator conservation in agricultural landscapes.
between all relevant stakeholders and will ultimately help to reduce nutritional stress for bee populations in modern agricultural landscapes.

Conclusion

In this study we conducted the first systematic review of nectar sugar quality bees can encounter in agricultural landscapes in- and off-field around the globe. We report that nectar sugar concentrations do not vary between regions or habitats with a median of around 40% nectar total sugar concentration. We have identified several crop genera providing nectar with sub optimal sugar concentrations for bees which could potentially benefit from alternative nectar sources during their mass flowering period. This dataset is only a first step toward integrating nectar sugar concentrations into bee management practices and we hope that this data resource will facilitate communication between all relevant stakeholders and ultimately help to reduce nutritional stress for bee populations in modern agricultural landscapes.

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Nectar sugar concentrations of bee visted flowers around the globe

Figure 1: Summarizes the total nectar concentration in percent in agricultural landscapes on a continental as well as global basis. We present data for Europe, North America, South America, Africa, Australia and overall (Global) for crop, weed and wild plant communities. Results of the statistical analysis panels (Kruskal Wallis (KW) chi², and p values) are presented in the upper left corner of the individual Panels.
Figure 2: The graph depicts the nectar sugar concentration of 52 sunflower varieties (*Helianthus annuus*) at two geographic locations in Bulgaria - Toschevow and Plovdiv area, measured during the years 1981-1986. Data taken from (Simidtschiev 1988).
Paired Wilcoxon test: \( V = 216, \ p < 0.0001 \)
Nectar sugar concentrations of plant genera

Figure 3: Shows the distribution of nectar sugar concentration among all genera for which more than 3 measurements were available. The red lines indicate the border of the optimal (65-35%), adequate (35-20%) and low sugar nectar concentration (<20%). Crop genera are marked in red.
KW test: chi−squ = 109.68, p < 0.0001
Table 1 (on next page)

Summary statistics of nectar sugar concentrations

Table 1.: Summary statistic of the sugar concentration [%] of crop, weed and wild plant communities across the globe
| Region      | Community | N   | median | mean  | 10th Percentile | 25th Percentile |
|------------|-----------|-----|--------|-------|-----------------|-----------------|
| Global     | ALL       | 322 | 40     | 41.0  | 25              | 32              |
|            | Crop      | 151 | 39.7   | 39.2  | 24              | 32              |
|            | Weed      | 30  | 39.8   | 41.6  | 30.5            | 33.6            |
|            | Wild      | 141 | 41     | 32    | 25              | 32              |
| Europe     | ALL       | 236 | 39.7   | 40.3  | 24.9            | 32.3            |
|            | Crop      | 144 | 39.9   | 39.4  | 24.1            | 32.9            |
|            | Weed      | 30  | 39.8   | 41.6  | 30.5            | 33.6            |
|            | Wild      | 62  | 39.3   | 41.7  | 24.9            | 29.9            |
| North America | ALL   | 240 | 40     | 40.9  | 25              | 32.7            |
|            | Crop      | 145 | 40     | 39.6  | 24.1            | 33              |
|            | Weed      | 30  | 39.8   | 41.6  | 30.5            | 33.6            |
|            | Wild      | 65  | 44     | 43.8  | 25.3            | 32.3            |
| South America | ALL | 234 | 40     | 41.3  | 26.4            | 33.9            |
|            | Crop      | 136 | 40     | 40.8  | 28.3            | 34.9            |
|            | Weed      | 18  | 41.7   | 42.5  | 32.9            | 37              |
|            | Wild      | 80  | 40     | 42    | 26              | 32              |
| Africa     | ALL       | 168 | 41     | 41.9  | 27.5            | 34.9            |
|            | Crop      | 133 | 40     | 40.9  | 28.5            | 35              |
|            | Weed      | 13  | 40     | 42.8  | 32.8            | 34              |
|            | Wild      | 22  | 51.8   | 47.6  | 23.3            | 34              |
| Asia       | ALL       | 211 | 40     | 40.9  | 26              | 33              |
|            | Crop      | 141 | 40     | 40    | 25.8            | 34              |
|            | Weed      | 25  | 43.4   | 42.5  | 31.7            | 34.7            |
|            | Wild      | 45  | 40     | 42.9  | 25.4            | 32.3            |
| Australia  | ALL       | 203 | 40     | 40.9  | 26              | 33              |
|            | Crop      | 139 | 40     | 40    | 25.8            | 43              |
|            | Weed      | 24  | 39.8   | 41.6  | 31.4            | 33.4            |
|            | Wild      | 40  | 40.8   | 43.6  | 25.9            | 32.5            |
