Remote Sensing and Reflectance Profiling in Entomology

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Abstract

Remote sensing describes the characterization of the status of objects and/or the classification of their identity based on a combination of spectral features extracted from reflectance or transmission profiles of radiometric energy. Remote sensing can be benchtop based, and therefore acquired at a high spatial resolution, or airborne at lower spatial resolution to cover large areas. Despite important challenges, airborne remote sensing technologies will undoubtedly be of major importance in optimized management of agricultural systems in the twenty-first century. Benchtop remote sensing applications are becoming important in insect systematics and in phenomics studies of insect behavior and physiology. This review highlights how remote sensing influences entomological research by enabling scientists to nondestructively monitor how individual insects respond to treatments and ambient conditions. Furthermore, novel remote sensing technologies are creating intriguing interdisciplinary bridges between entomology and disciplines such as informatics and electrical engineering.

INTRODUCTION

To most people, remote sensing refers to imaging- and reflectance-based surveying mounted on airborne devices and vehicles such as airplanes or satellites. Here, we follow a much broader definition of remote sensing: "the measurement or acquisition of information of some property of an object or phenomenon by a recording device that is not in physical or intimate contact with the object or phenomenon under study" (60). Consequently, even imaging through a microscope may be considered a type of remote sensing. In many remote sensing applications, the data are collected in parts of the radiometric spectrum that are not detectable by the human eye. The common denominator of most studies reviewed in this article is that arthropods were studied and one or more types of remote sensing technologies were involved. Many aspects of remote sensing are not covered here, but we attempt to cover what was considered of most relevance to a broad spectrum of entomologists with interest in incorporating remote sensing into their research programs. We wish to emphasize that entomological remote sensing is expanding in many directions and creating intriguing opportunities for collaborative research between entomology and disciplines such as informatics and electrical engineering.

Background and Context

Numerous important reviews (29, 71, 111, 117, 156) and textbooks (54, 60, 61, 124) describe the theory and applications of remote sensing, and it has been an established research discipline for about four decades (12, 147). It was Isaac Newton who discovered that light could be separated into a spectrum of colors, and approximately 100 years later, James Clerk Maxwell discovered that light as we see it is part of a very wide radiometric spectrum (113). Here, we review research on the acquisition and analysis of surface reflectance profiles, as use of transmission-based remote sensing applications has been limited. However, the same concepts, challenges, and assumptions are associated with successful use of reflectance and transmission profiles. Reflectance profiles represent the radiometric energy reflected by an object in a series of spectral bands. If an image is acquired, then each pixel is associated with a reflectance profile. An acquired reflectance profile is always relative to and determined by the combination of (*a*) the radiometric energy source used to elicit a reflectance profile, (*b*) the spectral and spatial sensitivity of the sensor used to acquire the reflectance data, and (*c*) calibration and processing steps involved in the photogrammetric process (46). The fundamental objective in remote sensing is to differentiate objects on the basis of a combination of spectral features extracted from reflectance profiles, and this endeavor is based on two fundamental assumptions: (*a*) It is possible to control for environmental heterogeneity (i.e., through calibration) so that spectrally repeatable reflectance profiles can be acquired from a given object over time and space, and (*b*) a given object is associated with unique reflectance profile features, such that even very similar objects (such as insect specimens of the same species) can be distinguished from all other objects belonging to different categories (different species, or males and females, age classes, and difference in mating status) or individuals exposed to different experimental treatments.

Spatial Resolution of Reflectance Data

An important aspect of remote sensing is the size of the area from which reflectance profiles are acquired. This area is the same as the pixel size in an image, and it determines the spatial resolution. Spatial resolution of pixels markedly influences the ability of scientists to accurately classify both airborne and benchtop remote sensing data (32, 65, 137, 158). If the pixel size is considerably larger than the size of target objects, then reflectance profiles are mixed (originating from more than one object), and that will likely compromise classification accuracies. Imaging software engineers have developed numerous approaches to fragment pixels (1, 55) and to artificially increase the spatial resolution of one imaging source through the use of a second type of imagery as part of a process called image fusion (35, 128). Despite these classification solutions, it is generally recommended that the spatial resolution be high enough to avoid mixed pixels and then averaged as part of spatial binning (reducing the spatial and spectral resolutions of hyperspectral imaging data) of input data (42, 65, 158). However, acquisition of reflectance data at a spatial resolution high enough to avoid mixed pixels becomes a serious challenge when remote sensing data are acquired from small plants, such as newly established crop plants, and from cereals or other plants with partially vertical leaves (and therefore have a small footprint when imaged from above). Low spatial resolution also becomes a serious challenge when large areas such as forests are monitored with airborne remote sensing systems and the goal is to detect individual trees stressed by insect activity (36).

Spectral Resolution of Reflectance Data

Intuitively, spectral resolution (defined as the number spectral bands in the reflectance profile) is positively associated with the ability to differentiate objects, so that classifications based on hyperspectral imagery (hundreds of spectral bands) generally outperform those derived from multispectral imagery (3–12 spectral bands) (148). However, there are comparative studies in which both multispectral and hyperspectral systems enabled investigators to accurately classify and detect biotic stressors in crops (149). Furthermore, experimental benchtop remote sensing studies suggest that both spatial and spectral binning may partially improve the ability to detect stress responses (94, 158). Possible constraints associated with acquiring remote sensing data at a high spectral resolution include increased equipment costs, data acquisition at lower spatial resolution (see below), data storage constraints, and, in airborne remote sensing, a lack of powerful airborne devices with higher pay load. So increasing the spectral resolution may have considerable practical and logistical trade-offs. Despite these constraints, there seems to be a strong trend in applied research toward increasing the use of hyperspectral imaging systems with several camera systems commercialized by a growing number of companies, including Surface Optics Corp., Galileo Avionica, BAE Systems, Bodkin Design and Engineering, Headwall Photonics, NovaSol, SphereOptics, and Resonon.

Spectral Repeatability of Reflectance Data

In airborne remote sensing applications, sunlight is almost exclusively the radiometric energy source, and diurnal and seasonal variations in sun angle, cloud cover, and atmospheric composition impose considerable challenges and limitations on acquiring high-quality airborne remote sensing data. Although a wide range of correction techniques partially account for nonconstant light conditions during airborne remote sensing (30, 82), numerous studies highlight the challenges associated with a nonconstant radiometric energy source, and how it may lead to low spectral repeatability (8, 107) and low input-data robustness (90) and therefore loss of classification accuracy. Benchtop remote sensing data are acquired under controlled imaging conditions, so the spectral repeatability and robustness of these data sets are comparatively higher. However, challenges associated with low spectral repeatability also apply to benchtop remote sensing (90). A key challenge in successful applications of remote sensing technologies is to minimize the variability in signal levels from the radiometric energy source and to include comprehensive calibration methods as part of the initial data-processing steps. The importance of this problem was illustrated in an experimental study of potted maize (*Zea mays*) plants with and without sugarcane borer (*Diatraea saccharalis*) infestation, and with hyperspectral imaging data from the same plants acquired under two light regimes, exposed to direct sunlight and under a greenhouse shade cloth (94). Despite the use of individual white calibration of all hyperspectral images, a classification model based on data acquired one day could not be used to successfully predict sugarcane borer infestation levels on the same plants (*a*) eight days earlier and under the same light regime or (*b*) on the same day but under a different light regime. Thus, the exact same plants were imaged twice on the same day, and white calibration was performed for each hyperspectral image and separately for the two light regimes. Despite thorough white calibration, the difference in light conditions (outside versus inside a shaded greenhouse) was enough to significantly change the acquired reflectance response from the potted maize plants, so that data from one regime could not be used to describe data acquired under the other light regime.

Spatial resolution affects the repeatability of remote sensing data. That is, leaf reflectance profiles acquired with hand spectrometers or ground-based hyperspectral imaging cameras may vary from those obtained with airborne remote sensing systems (24, 53, 130, 151). Such differences are attributed to a range of factors, including atmosphere, shadow pattern, background composition, and instrument noise (24). Thus, reflectance data are likely to be scale dependent and profiles developed at one geographical scale may not transfer to larger or smaller scales. As a consequence of the many factors affecting the quality of remote sensing data, development of reliable and robust radiometric calibration procedures to increase the repeatability of features extracted from reflectance profiles is therefore one of the most important challenges associated with practical adoption of remote sensing technologies for, for instance, detecting insect-induced stress in crops (107). Challenges with low repeatability of features extracted from reflectance profiles are of particular importance when the objective is to accurately detect subtle levels of insect-induced stress as part of an early-warning system. Thus, there is a great need for close research collaboration among field entomologists, crop physiologists, electrical engineers, and computer scientists to develop calibration and data-processing procedures to enable classifications with both high sensitivity and robustness (90, 107).

Penetration Depth of Reflectance Data

Despite the considerable research effort among natural scientists on the use of remote sensing technologies, only a limited number of studies have described the penetration depth of remote sensing data acquired from different objects. Penetration depth may be defined as the depth needed for the radiometric energy to be reduced by approximately 37% (145). Penetration depth is an important aspect of remote sensing because it determines (*a*) which wavelength range would be expected to show the strongest reflectance response (based on which tissue layers were most affected by the given treatments) when acquiring surface reflectance data, and (*b*) how the reflectance data should be interpreted. In general, penetration depth is a function of the wavelength in free space, the radiometric energy source, and the refractive index (155). It is beyond the scope of this review to dwell into the high-powered physics involved, but it has been shown that the penetration depth of radiometric energy into fruits and vegetables is several millimeters, and that it varies with wavelengths. For instance, the penetration depth of radiometric energy was up to 4 mm in spectral bands from 700 to 900 nm, and it was 2–3 mm in spectral bands from 900 to 1,900 nm (68). A specific study of penetration depth into fruit concluded that penetration depths reached 7.1 mm at 535 nm in plums (*Prunus* sp.) and 13.8 mm at 720 nm for zucchini (*Cucurbita pepo* var. *cylindrica*) (112). This study showed that maximum penetration depths may reach 18.3 mm (apple) (*Malus* sp.) and 65.2 mm (zucchini). One potential implication of penetration depth in applications of remote sensing technologies is that if an object (such as a crop leaf or a small insect) is only a few millimeters thick, then it becomes important to consider the possible effects of substrates or objects below the surface from which reflectance data are acquired. This may be a serious challenge in airborne remote sensing applications, as crop leaves are only a few millimeters thick, and it is virtually impossible to control for superimposed leaves and/or effects of soil features underneath the crop canopy.

Penetration depth has a profound impact on the spectral repeatability of both airborne and benchtop applications of remote sensing technologies. In airborne applications, it is well known that both soil background and layers of leaves within a canopy affect acquired reflectance data (60). Although not studied extensively as part of benchtop applications, constant background materials and colors, especially from small and/or thin target objects, may be important to the acquisition of reflectance data. Finally, aspects associated with penetration depth imply that reflectance profiles acquired from either plant tissues or insect bodies are not determined exclusively by the epicuticular structure but also by the physiological and biochemical composition of internal tissues.

CLASSIFICATION OF REMOTE SENSING DATA

Numerous methods have been used to classify entomological remote sensing data, including analysis of reflectance values of single spectral bands (93, 98), spectral band indices (17, 24, 79, 85, 90, 95), partial least square (PLS) (2, 4, 63), principal component analysis (PCA) (90, 102), linear discriminant analysis (LDA) (94), decision trees (37), neural network (73), support vector machine (SVM) (111), variogram analysis (90–93, 95, 97, 100), and spatial pattern analysis (5–7). Sometimes reflectance values of spectral bands are transformed prior to classification, and the most common transformations include conversions of reflectance profiles into first- or second-order derivatives (26). Another conversion approach is to divide reflectance data from one treatment with average reflectance data from controls to obtain a relative sensitivity estimate of difference or treatment response (116). Regarding classification of remote sensing data, one of the simplest (and widely used) approaches is to generate spectral band indices (8), in which the number denotes the wavelength in nanometers and R denotes reflectance (so that 750R means reflectance at 750 nm). NDVI [normalized difference vegetation index (750R − 705R)/(750R + 705R)], PRI [photochemical reflectance index (531R − 570R)/(531R + 570R)], and SI [stress index (693R/759R)] are three examples of commonly used spectral indices. Willers et al. (144) used NDVI maps derived from multispectral data supplemented with knowledge of crop and soil conditions to define habits of tarnished plant bug (*Lygus lineolaris*) in cotton (*Gossypium hirsutum*) and to optimize field scouting. In addition, a wealth of simple two-spectra band indices are used to estimate chlorophyll content in leaves, including 430R/680R (47), 672R/550R (25), 710R/760R (18), and 750R/550R (41). Finally, a large body of research describes how spectral band indices are used to quantify nitrogen content in leaves (89, 160). Such indices are convenient, but they do not take advantage of the detailed reflectance information acquired with most spectral sensors with higher spectral resolution, and the indices are quite sensitive to even minor levels of heterogeneity within target objects (97). In addition, spectral band indices have been less accurate than other classification methods (90, 95).

Multispectral and hyperspectral data from entomological remote sensing research are commonly classified on the basis of methods in which reflectance values of numerous spectral bands are used (i.e., PLS, LDA, PCA, neural networks, and SVM). That is, it is inherently assumed that subtle differences among classes are most accurately detected and classified when they are based on changes in reflectance in a combination of spectral bands. In benchtop remote sensing of individual insects, reflectance profiles acquired from insect bodies are considered indicators of physiological, biochemical, or taxonomic differences among specimens. So if a particular treatment causes a significant change in the insect's metabolism, it is assumed that reflectance profiles change accordingly. This assumption is supported by the current knowledge about penetration depth of radiometric energy in the spectral bands (see above).

In remote sensing studies of insect herbivory, a large body of research has demonstrated that the overall physiological effects of insect herbivory (as well as the general effect of many other abiotic and biotic plant stressors) adversely affect photosynthesis and therefore lead to an increase in leaf reflectance (reduced light absorption by leaf pigments) (19, 111). Plant pigments have maximum reflection peaks at particular wavelengths (34, 58): chlorophyll *a* (430 nm, 662 nm, and 680 nm), chlorophyll *b* (448 nm and 642 nm), and carotenoids (448 nm and 471 nm). Increased reflectance in these spectral bands may be considered indicative of insect herbivory adversely affecting the plant's ability to perform photosynthesis.

However, there are important exceptions to the general notion that insect herbivory increases leaf reflectance. For instance, greenbug (*Schizaphis graminum*) infestations in wheat (*Triticum aestivum*) caused a decrease in reflectance in the UV-light portion of the spectrum compared with reflectance from noninfested control leaves, whereas stress induced by Russian wheat aphid (*Diuraphis noxia*) herbivory caused an increase in reflectance (116). In a study of wheat plants exposed to experimental frost stress, levels of reflectance decreased in response to the abiotic stress, which was further associated with increased potassium content in wheat plants and increased suitability of frosted wheat plants as host to bird cherry-oat aphids (*Rhopalosiphum padi*) (66). These examples highlight important nonlinear relationships between crop response to stressors and leaf reflectance, and they may be associated with a range of (over-)compensatory mechanisms by plants exposed to abiotic and biotic stressors (134). Our current understanding of direct relationships between leaf reflectance and the physiological consequences of exposure to stressors is limited, and we argue that more multidisciplinary collaboration among entomologists, crop physiologists, and remote sensing specialists is needed to address this research gap.

Risks of Model Overfitting and the Importance of Independent Validation

In all commonly used multiband classification methods, a large number of spectral bands are used initially to calculate factors (PLS), discriminant scores (discriminant analysis and PCA), or vectors (SVM). In the initial phase of a multiband classification, preprocessing steps are often included to develop a few relative axes of variation, encompassing the main variation captured by the reflectance values of a large number of spectral bands. That is, many of the spectral bands within the acquired reflectance profile may not contribute significantly to the given classification, so they must be identified and excluded. It is important to reduce the number of spectral bands included in a classification algorithm of remote sensing data because (*a*) developing classifications based on only a subset of spectral bands often increases the classification accuracy (94); (*b*) developing classification methods based on large numbers of spectral bands increases the risk of model overfitting due to the Hughes phenomenon (43, 77) or violation of the principle of parsimony (45); and (*c*) classification algorithms based on reflectance values of large numbers of spectral bands increase computer processing requirements (158), which may be a restriction when the purpose is to develop reflectance-based systems with high data throughput. If the reflectance data contain reflectance values of a number of spectral bands, which are similar to the number of observations, then there is a high risk of model overfitting (28, 62). As a hypothetical example, suppose remote sensing is used to assess insect-induced stress responses in experimental field plots with a crop grown under three irrigation regimes, "a," "b," and "c." We assume that no pesticides are used and that all stressors can be controlled. To study this, 30 experimental field plots could be established, in which 15 (five replications from each irrigation regime) are experimentally infested and the remaining 15 are kept as non-infested control plots. Remote sensing data collected at four time points after experimental infestation could be used to address how early the crop stress is detectable on the basis of reflectance data and which spectral bands show the strongest response to insect-induced stress. Insect infestation is the response variable and may be either dichotomous (yes/no) or on ordination scale (if insect density estimates were conducted at each time point), and reflectance values of the spectral bands are used as explanatory variables. In this example, 120 imaging data sets (30 plots $\times$ 4 time points) are collected, so the data set would consist of 120 average reflectance profiles across treatments and over time. If the spectral sensor used collects reflectance values from much more than 100 spectral bands, then the number of explanatory variables (spectral bands) would be either close to or higher than the number of observations, and that means a high risk of model overfitting. One main consequence of model overfitting is that the given classification model performs poorly and inconsistently when applied to independent validation data.

There are several ways to minimize the risk of model overfitting; one way is spectral binning, which refers to averaging adjacent spectral bands (158). Spectral binning not only reduces the risk of model overfitting, but it may also increase classification accuracy (94, 158). Overfitting is likely to occur when the number of explanatory variables (in this case, spectral bands) is higher than $(N - G)/3$, where N is the number of samples and G is the number of treatment classes (28). So in the theoretical example above, the number of spectral bands should be reduced to 38 [$(120 - 6)/3 = 38$]. When developing methods to classify remote sensing data, it is paramount that the acquired reflectance data are divided into two parts, a training data set (typically 67–80% of the data) to develop the classification model and an independent validation data set (typically 20–33% of the data), which are used to quantify the accuracy of the classification model. In the theoretical example described above, randomly selecting 25% of the data for validation would mean that the classification would be based on 90 average reflectance profiles (instead of 120), so the number of spectral bands used in the classification model should not exceed 28 [$(90 - 6)/3 = 28$] (see 28).

Spatial-Based Classification Methods

Owing to concerns about spectral repeatability and the risk of model overfitting of multiband-based classifications, we highlight classification methods in which the spatial structure of remote sensing data sets is analyzed. In these classification approaches, spectral resolution is less important; instead, the spatial association of reflectance values from one or a few spectral bands among neighboring pixels is analyzed. Backoulou et al. (5–7) used spatial pattern analysis to distinguish distributional patterns of an insect pest based on spatial variation in plant stress detected in multispectral imagery caused by the insect's inherent patchy spatial distribution in the field. Insects have species-specific spatial distributions within a particular ecological habitat (132), and their outbreaks in crops are frequently spatially aggregated (64, 99, 121, 146). In addition, Russian wheat aphid showed patchy spatial distributions in wheat fields (5, 6). Thus, the spatial resolution of the remote sensing data must be high enough to detect pest-induced stress at the plant and ideally leaf levels. Another spatial-structure classification method is based on variogram analysis of reflectance values of individual spectral bands (57, 75), in which the parameters derived from regression fits to variograms are used as indicators of the particular target object (90–93, 95, 97, 100).

A series of field-scale airborne remote sensing studies have described the use of spatial variation NDVI maps to distinguish infestations of Russian wheat aphid and greenbug from other common stressors in wheat plants (5–7). The approach does not depend on detailed spectral profiling; instead, it relies on detecting stress in wheat from variation in NDVI within the field and using spatial pattern metrics to differentiate stress caused by the aphids from other factors causing stress. A similar feature-based classification approach has been applied to airborne multispectral data of forest trees, in which linear spectral mixture models are used to determine the spatial distribution of nonphotosynthetically active vegetation, shade, and soil, and pixels with high loadings of these features are associated with insect-induced stress (74, 106). A potential drawback to this feature-based approach is that NDVI imagery must be classified into stressed versus nonstressed categories within a GIS, a process that does not lend itself to automation. Owing to the logistics of coordinating crop management practices, and because of rapid growth rates of many pests, near real-time data processing is a requirement for successful integration of remote sensing technologies into pest management systems. However, if robust and reliable classification algorithms can be developed and successfully tested, then integration of remote sensing technologies into pest management systems has considerable potential and may greatly decrease response time and enable development of highly targeted and optimized management strategies.

FIELD-BASED REMOTE SENSING

A large and interesting body of research exists on the use of vertically projected radar systems under field conditions (20). In these applications of remote sensing, the radar beam's plane of polarization is rotated and three embedded signals are used to identify and quantify insect species (21): (*a*) maximum and minimum radar reflectivity, (*b*) estimates of body mass, and (*c*) wingbeat frequency. These applications of radar-based remote sensing have provided fascinating quantitative insight into the diurnal rhythms and long-term dynamics of migrating and dispersing insects across a wide range of orders (10, 11, 22, 118, 127). However, most field-based applications of remote sensing technologies concern detection and quantification of plant responses to arthropod herbivory or quantification of potential host plant distributions. In other words, features in reflectance data acquired from plants are used to indicate on the basis of plant species composition where insects may already be feeding (causing stress to plants) or where they may become established. The spatial mapping of emerging insect-induced stress can be used to predict when and where economic loss of crops (including forest trees) may take place.

Remote Sensing of Host Plant Responses to Arthropods

One of the main drivers for the implementation of airborne remote sensing technologies into the agricultural sector is the potential time saved by automatizing crop monitoring (5, 16, 135). With the recent surge in food commodity prices and the growing interest and concern about food security and agricultural sustainability, technologies such as airborne remote sensing systems are needed to improve the productivity of food production systems (9, 15). A large body of research exists on the use of handheld spectrometers and ground-based multispectral and hyperspectral imaging technologies to detect and quantify arthropod-induced stress in crops (85, 86, 91, 94, 95, 116, 150, 151). Airborne platforms include satellites, manned aircraft, and unmanned aerial vehicles (UAVs) (also called unmanned aerial systems, UAS).

Three remote sensing technologies mounted on airborne devices have received considerable attention: (*a*) lidar (light detection and ranging), (*b*) satellite imagery, and (*c*) multispectral and hyperspectral systems. Lidar measures the distance between the sensor and a surface target, and it has been used to characterize and estimate the three-dimensional structure and biomass of crop plant canopies, respectively (72, 111). Lidar has been used to characterize defoliation by pine sawflies (*Neodiprion sertifer*) of Scots pine (*Pinus sylvestris*), but lidar data correlated only weakly with multispectral MODIS (moderate resolution imaging spectroradiometer) data (36). However, lidar data were used successfully to measure plant biodiversity and to identify correlations with forest beetle biodiversity (88). Satellite imagery is well suited to automated mapping over large geographic areas, such as monitoring insect defoliation in forests over multiple years and expansive areas (36, 120). Even with the newest source of commercially available satellite imagery (e.g., Quickbird, Worldview-2, and GeoEye-1), practical constraints for use of satellite imagery in agricultural insect pest management include slow data delivery time to end users, fixed orbital cycles with generally low temporal resolution, generally low spatial resolution, and weather dependency (challenges imposed by cloud cover) of image quality (111). Numerous studies describe the use of airborne multispectral and hyperspectral reflectance data acquired from crop plants (17, 19, 86, 131, 150, 152, 156) and forests (130) under arthropod-induced stress.

The Future of Remote Sensing of Host Plant Responses

Increasingly miniaturized optical sensors and the recent technological advancements in UAV technologies are expected to revolutionize spatial ecology, including arthropod-induced stress detection in food production systems (3). Currently, widespread use of UAVs to acquire remote sensing data is facing some practical constraints associated with payload limitations (weight of imaging system), short flight duration (limited battery power), and flight stability (156). Zhang et al. (157) highlighted equipment costs, operational logistics, and lack of experienced personnel as important limiting factors regarding the use and adoption of airborne remote sensing in agriculture. Although the technical limitations to widespread applications and commercial use of airborne remote sensing technologies are few and solvable, important regulatory hurdles must be addressed (39). In addition, possible constraints are associated with reflectance data calibration and accurate georeferencing of high spatial resolution imaging data. After acquisition of multispectral and hyperspectral imaging data are acquired, there may be considerable challenges associated with instrument calibration, calibration for sun angle and variability in cloud cover, atmospheric correction, vignetting and line-shift correction, band-to-band registration, and frame mosaicking (67, 156). It may be challenging to accurately classify remote sensing data under real-world conditions due to simultaneous interactions among various abiotic and biotic stressors. For example, upon analyzing spectral reflectance data, Yang et al. (150) experienced difficulties differentiating stress to wheat induced by greenbugs from that induced by moisture deficit, and Reisig & Godfrey (115) could not accurately detect nitrogen deficiency in cotton due to stress by cotton aphids (*Aphis gossypii*).

Despite important challenges, remote sensing technologies will undoubtedly be of major importance in optimized management of agricultural systems in the twenty-first century; for example, remote sensing–based crop management is being adopted to detect insect infestations, such as fall armyworms (*Spodoptera frugiperda*) in wheat (157). As discussed by Patterson & Brescia (105), two broadly defined developments will likely have far-reaching positive impacts: (*a*) on-board processing in airborne remote sensing systems and (*b*) integration of individual sensors into networks. On-board processing in airborne remote sensing systems broadly refers to the system's ability to make decisions while in flight and therefore obtain high-quality data (39). As an example, without on-board processing the UAV is flying continuously at a predetermined altitude and flight path, and the data are processed and classified after the device has landed. On-board processing may enable the UAV to make immediate changes in both flight path and altitude (for instance, changing to a lower flight altitude to obtain reflectance data at a higher spatial resolution) if a certain stress reflectance signal is detected. Regarding synchronization of sensors, flying multiple UAVs simultaneously and in synchronized patterns can be used to acquire multispectral or hyperspectral data at a high spatial resolution and cover a large area during short periods of time. In addition, future investigations may integrate stationary sensors of crop stress with data from weather stations, soil probes, and automated insect traps so that researchers can carefully monitor crop development and predict risks of pest infestations. And farmers and crop consultants may receive this integrated and analyzed information on their smartphones, or it may upload directly to unmanned tractors and trigger an automated pesticide spray application.

BENCHTOP REMOTE SENSING

High spatial and spectral resolution remote sensing data acquired under controlled conditions (lighting, abiotics, projection angle, distance between objects and lens) are becoming increasingly important within a wide range of entomological research disciplines, such as systematics, toxicology, physiology, and behavior, but also new research disciplines such as photonics (153) and phenomics (48). Photonics refers to research and technology involving emission, control, and detection of light photons, so it relates to the hardware aspects of benchtop remote sensing. Phenomics refers to biological research into phenotypic responses by organisms and involves both detailed analyses of genetic and molecular data as well as in-depth characterization of physical traits and responses to environmental conditions. Benchtop remote sensing is highly relevant to detailed and quantitative characterizations of physical traits in organismal responses to environmental conditions.

Arthropod Systematics

Awareness about biosecurity risks associated with invasive insect species continues to grow (108). Risks of invasive insect species are increased by tourism and import/export of goods and machinery, as well as climate change (109). Countries and trade organizations are therefore developing appropriate quarantine and inspection policies and procedures. Insect identification is part of these quarantine and inspection efforts, and benchtop remote sensing technologies to reduce processing time and automate some aspects of inspection for invasive insect species are being developed. A decision tree classification model based on simple (three spectral bands) digital imagery of wings and aculei was used to classify three closely related species of fruit flies [*Anastrepha fraterculus*, *A. obliqua*, and *A. sororcula* Zucchi] for which classification accuracy was approximately 98% (37). Nguyen et al. (103) described a new imaging system that can be used to develop digitized three-dimensional models of insect species. Such digitized models of insects are easy to share and store and may therefore reduce the need to ship specimens among taxonomists and increase the availability of insect reference collections. Different reflectance-based spectroscopy methods have enabled researchers to classify a wide range of insects, including species of stored-grain insects (126), two species of fruit flies (*Drosophila melanogaster* and *D. simulans*) (4), tobacco budworm (*Heliothis virescens*), and corn earworm (*Helicoverpa zea*) (59), and Klarica et al. (63) used imaging spectroscopy to discriminate cryptic species of ants (*Tetramorium caespitum* and *T. impurum*). Nansen et al. (93) demonstrated that three species of minute juvenile egg parasitoids (*Trichogramma* spp.) developing inside moth host eggs could be accurately classified on the basis of the reflectance profiles acquired from the host eggs. Using two types of radiometric energy sources (UV and white light), Zschokke (161) analyzed the reflectance of 21 spider species and their corresponding webs and suggested that the reflectance features of the species-specific webbing structures (stabilimenta) are likely associated with predator defense. Finally, there is a study of how reflectance profiling has been used in taxonomic studies of fossil insects (83).

Cryptic Insect Infestations

As part of food safety and quality control in the food industry, there is a growing body of research on use of hyperspectral imaging technologies acquiring reflectance data within the 400–1,000 nm range. The approach has been used to detect damage and internal infestation in food products, including field peas (*Pisum sativum*) (100, 158), wheat kernels (*Triticum aestivum*) (125, 126), soy beans (*Glycine max*) (52), and jujubes (*Ziziphus jujuba*) (139, 140). In addition, thermal imaging (reflectance in the 8–12 μm range) has been used to detect infestations by a stored grain beetle (*Cryptolestes ferrugineus*) inside wheat kernels (80) and infestations by insects in a wide range of other food products (136). A recent study of seven species of evacanthine leafhoppers (Hemiptera: Cicadellidae) described integration of alpha taxonomy, mitochondrial DNA, and hyperspectral reflectance profiling (37 spectral bands from 411 to 870 nm) (141). This study demonstrated that species identified on the basis of alpha taxonomy and mitochondrial DNA could be distinguished on the basis of hyperspectral reflectance profiling with a classification accuracy of approximately 91.3%. Thus, hyperspectral reflectance profiling is as a possible tool for rapid and nondestructive identification of closely related and cryptic insect species (141).

Insect Physiology and Phenomics

Benchtop remote sensing enables nondestructive characterization of insects and quantifications of how individual organisms perform based on their genetic code and in response to environmental conditions (i.e., phenomics). Because phenotypic responses by insect individuals are often complex, development of image-based systems to detect and quantify phenotypic responses are important aspects of phenomics projects (13). Results from synchrotron X-ray imaging studies may increase our current knowledge about the function of air sacs, hemolymph transport, pulsatile organs, pharyngeal pumps, digestive systems, leg joints, and feeding mechanisms of biting and fluid-feeding insects (see 143 for a review). Synchrotron X-ray imaging has also been used extensively to determine the location, movement, and changes in chemical form of nutritional elements and potential toxicants (Cl, K, Ca, Fe, and Zn) in urine and hemolymph samples of a hemipteran insect model (*Rhodnius prolixus*) (81). Benchtop remote sensing technology has been used to study the distribution and chemical forms of arsenic (As) in body portions of life stages of two aquatic insects (the midge *Chironomus riparius* and the mosquito *Culex tarsalis*) (87). In addition, synchrotron X-ray imaging has been used to study the physiology of insect flight muscles (31, 56, 138).

Mietchen et al. (84) studied cold adaptation in larvae of two gall-producing insects, *Epiblema scudderiana* and *Eurosta solidaginis*. No staining or chemical preparation of the larvae was performed. The authors exposed individual larvae to 0, −20, −35, and −70°C, and for each temperature treatment, they obtained magnetic resonance images and corresponding reflectance profiles. The authors developed three-dimensional larval anatomy models and clearly visualized the difference in quantities and distribution of liquid water and of the endogenous cryoprotectants across temperature treatments. The three-dimensional larval anatomy models provided new and quantitative insight into the mechanisms by which insect larvae adapt to cold temperature regimes, and are therefore an excellent example of a remote sensing–based phenomics study.

As described above, the penetration depth of radiometric reflectance signals in spectral bands from 400 to 1,000 nm appears to justify more conventional reflectance-based applications of benchtop remote sensing. Moreover, near-infrared spectroscopy has been used to age-grade laboratory-reared mosquito species (*Anopheles* spp.) (122, 123) and biting midges (*Culicoides sonorensis*) (114). Aw et al. (4) found that near-infrared spectroscopy of two species of fruit flies (*Drosophila melanogaster* and *D. simulans*) could be used to assess their gender, age them into two age-classes, and determine whether they were infected with *Wolbachia* (classification accuracies ranged from 62% to above 90%). Webster et al. (142) used near-infrared spectroscopy to successfully differentiate mated and unmated honey bee queens on the basis of differences in reflectance profiles acquired from the bee abdomen. Thus, they provided a noninvasive and rapid method for distinguishing between mated and unmated queens. Near-infrared spectroscopy has also been used in physiological studies of vision in honey bees (*Apis mellifera*) and orb-weaving spiders (*Nephila pilipes*) (23).

A recent study with adult beetles from two species, maize weevils (*Sitophilus zeamais*) and larger black flour beetles (*Cynaus angustus*), described how temporal changes in body reflectance were detected in response to two killing agents (entomopathogenic nematodes and an insecticidal plant extract) (96). The detected changes in body reflectance occurred after exposure times, which coincided with published exposure times and known physiological responses to each killing agent. The results from this reflectance-based study underscore the potential of hyperspectral imaging of the insect body as an approach to nondestructively and noninvasively quantify stress detection. The role of epicuticular hydrocarbons in both intra- and interspecific communication among insects is well established (50), as they tend to vary (*a*) among closely related species (33, 119), (*b*) in relative (40) or actual (51) composition among males and females within a species, (*c*) among life stages and age of adults (14, 49, 70, 119, 159), (*d*) among eusocial individuals with different tasks (38, 104), (*e*) according to mating behavior and status (49, 51, 129), and (*f*) in response to environmental conditions (27, 49, 51). Owing to the intra- and interspecific variations in epicuticular hydrocarbon profiles, it seems reasonable to assume that reflectance profiles acquired from insect surfaces may be used to study physiological responses by insects and quantify differences among species.

Insect Behavior

To test a hypothesis describing *Morpho* butterfly mating behavior and predator avoidance behavior, Young (154) examined wing coloration and reflectance across the visible light spectrum. In salticid spiders, reflectance profiling has been widely used to describe mating behavior (76). Furthermore, reflectance data from 280 to 750 nm were analyzed, and Land et al. (69) demonstrated that a specific layering of chitin scales and an air gap created two specific reflectance peaks at 600 and 385 nm. These two reflectance peaks were found only in females and were considered responsible for the initiation and maintenance of the male's courtship display (69). Several studies have described the importance and potential of using reflectance profiling to nondestructively identify epicuticular hydrocarbons and combining this information with observational data within and among colonies of weaver ants (*Oecophylla smaragdina*) (101, 102). In a recent study of cicada sound production, hyperspectral imaging of forewing costae demonstrated significant differences between mute cicadas and those producing sound by the tymbal (78). Finally, behavioral preference studies with spider mites (*Tetranychus cinnabarinus*) (98) and aphids (*R. padi*) (66) showed how nutrient composition of crop leaves could explain host choices and that reflectance features could be used to predict the choices made by these herbivores.

CONCLUDING REMARKS

Few examples exist of commercial applications of airborne remote sensing for detecting and quantifying insect densities and distributions in large-scale anthropogenic and natural landscapes (157). However, irrigation (44), fertilization (89), weed detection (110, 133), and yield mapping (157) are just some crop management practices that are being transformed by remote sensing technologies. As on-board processing in UAV-based technologies and sensor networking become more advanced (39), researchers will widely utilize remote sensing technologies to detect and quantify insect densities and their distributions.

Remote sensing is highly suitable for integration into modern university teaching, as students with a strong inclination toward computer technologies may find it attractive and relevant to their future careers. Thus, remote sensing may not only directly affect and improve current crop management practices, it may also be a platform to increase the interests of companies and research institutions to develop commercial and innovative solutions for the agricultural sector. Challenges associated with spatial resolution and spectral repeatability of airborne remote sensing data are creating opportunities for intriguing collaborative research among scientists in the biological and agricultural sciences and fellow researchers in informatics and electrical engineering.

Benchtop remote sensing complements a wide range of more established entomological disciplines, and a rapidly increasing number of studies exist in which reflectance profiling of arthropods is used to quantify differences among closely related species. A range of imaging systems, such as synchrotron X-ray imaging, have provided detailed insights into important aspects of physiological studies and have proven to be valuable to phenomics studies of insects. Benchtop remote sensing will likely play a growing role in basic insect taxonomy and in the development of diagnostic monitoring of invasive species. Finally, as imaging technologies continue to evolve in the medical and military fields, which have access to large research budgets, there will undoubtedly be many basic and applied remote sensing spin-offs with important implications and prospects for entomological research.

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LITERATURE CITED

1. Akhtar N, Shafait F, Mian A. 2015. Futuristic greedy approach to sparse unmixing of hyperspectral data. *IEEE Trans. Geosci. Remote Sens.* 53:2157–74
2. Aldrich BT, Maghirang EB, Dowell FE, Kambhampati S. 2007. Identification of termite species and subspecies of the genus *Zootermopsis* using near-infrared reflectance spectroscopy. *J. Insect Sci.* 7:1–7
3. Anderson K, Gaston KJ. 2013. Lightweight unmanned aerial vehicles will revolutionize spatial ecology. *Front. Ecol. Environ.* 11:138–46
4. Aw WC, Dowell FE, Ballard JWO. 2012. Using near-infrared spectroscopy to resolve the species, gender, age, and the presence of *Wolbachia* infection in laboratory-reared *Drosophila*. *G3* 2:1057–65
5. Backoulou GF, Elliott NC, Giles K, Phoofolo M, Catana V. 2011. Development of a method using multispectral imagery and spatial pattern metrics to quantify stress to wheat fields caused by *Diuraphis noxia*. *Comput. Electron. Agric.* 75:64–70
6. Backoulou GF, Elliott NC, Giles KL, Phoofolo M, Catana V, Mirik M. 2011. Spatially discriminating Russian wheat aphid induced plant stress from other wheat stressing factors. *Comput. Electron. Agric.* 78:123–29
7. Backoulou GF, Elliott NC, Giles KL, Rao MN. 2013. Differentiating stress to wheat fields induced by *Diuraphis noxia* from other stress causing factors. *Comput. Electron. Agric.* 90:47–53
8. Baghzouz M, Devitt DA, Morris RL. 2006. Evaluating temporal variability in the spectral reflectance response of annual ryegrass to changes in nitrogen applications and leaching fractions. *Int. J. Remote Sens.* 27:4137–57
9. Beddington J. 2010. Food security: contributions from science to a new and greener revolution. *Philos. Trans. R. Soc. B* 365:61–71

10. Beerwinkle KR, Lopez JDJ, Schleider PG, Lingren PD. 1995. Annual patterns of aerial insect densities at altitudes from 500 to 2400 meters in east-central Texas indicated by continuously-operating vertically-orientated radar. *Southw. Entomol. Suppl.* 18:63–80
11. Beerwinkle KR, Lopez JDJ, Witz JA, Schleider PG, Eyster RS, Lingren PD. 1994. Seasonal radar and meteorological observations associated with nocturnal insect flight at altitudes to 900 meters. *Environ. Entomol.* 23:676–83
12. Billingsley FC. 1984. Remote sensing for monitoring vegetation: an emphasis on satellites. In *The Role of Terrestrial Vegetation in the Global Carbon Cycle: Measurement by Remote Sensing*, ed. GM Woodwell, pp. 161–80. New York: Wiley
13. Burleigh JG, Alphonse K, Alverson AJ, Bik HM, Blank C, et al. 2013. Next-generation phenomics for the Tree of Life. *PLOS Curr. Tree Life* doi: 10.1371/currents.tol.085c713acafc8711b2ff7010a4b03733
14. Butler SM, Moon RD, Hinkle NC, Millar JG, Mcelfresh JS, Mullens BA. 2009. Characterization of age and cuticular hydrocarbon variation in mating pairs of house fly, *Musca domestica*, collected in the field. *Med. Vet. Entomol.* 23:426–42
15. Camargo A, Molina JP, Cadena-Torres J, Jimenez N, Kim JT. 2012. Intelligent systems for the assessment of crop disorders. *Comput. Electron. Agric.* 85:1–7
16. Carrière Y, Ellsworth PC, Dutilleul P, Ellers-Kirk C, Barkley V, Antilla L. 2006. A GIS-based approach for areawide pest management: the scales of *Lygus hesperus* movements to cotton from alfalfa, weeds, and cotton. *Entomol. Exp. Appl.* 118:203–10
17. Carroll MW, Glaser JA, Hellmich RL, Hunt TE, Sappington TW, et al. 2008. Use of spectral vegetation indices derived from airborne hyperspectral imagery for detection of European corn borer infestation in Iowa corn plots. *J. Econ. Entomol.* 101:1614–23
18. Carter GA. 1994. Ratios of leaf reflectance in narrow wavebands as indicators of plant stress. *Int. J. Remote Sens.* 15:697–703
19. Carter GA, Knapp AK. 2001. Leaf optical properties in higher plants: linking spectral characteristics to stress and chlorophyll concentration. *Am. J. Bot.* 88:677–84
20. Chapman JW, Drake VA, Reynolds DR. 2011. Recent insights from radar studies of insect flight. *Annu. Rev. Entomol.* 56:337–56
21. Chapman JW, Reynolds DR, Smith AD. 2003. Vertical-looking radar: a new tool for monitoring high-altitude insect migration. *Bioscience* 53:503–11
22. Chapman JW, Reynolds DR, Smith AD, Riley JR, Pedgley DE, Woiwod IP. 2002. High-altitude migration of the diamondback moth *Plutella xylostella* to the U.K.: a study using radar, aerial netting, and ground trapping. *Ecol. Entomol.* 27:641–50
23. Chiao CC, Wu W-Y, Chen S-H, Yang E-C. 2009. Visualization of the spatial and spectral signals of orb-weaving spiders, *Nephila pilipes*, through the eyes of a honeybee. *J. Exp. Biol.* 212:2269–78
24. Coops NC, Stone C, Culvenor DS, Chisholm L. 2004. Assessment of crown condition in eucalypt vegetation by remotely sensed optical indices. *J. Environ. Qual.* 33:956–64
25. Datt B. 1998. Remote sensing of chlorophyll *a*, chlorophyll *b*, chlorophyll *a*+*b*, and total carotenoid content in *Eucalyptus* leaves. *Remote Sens. Environ.* 66:111–21
26. Dawson TP, Curran PJ. 1998. A new technique for interpolating red edge position. *Int. J. Remote Sens.* 19:2133–39
27. de Loof A, Huybrechts J, Geens M, Vandersmissen T, Boerjan B, Schoofs L. 2010. Sexual differentiation in adult insects: male-specific cuticular yellowing in *Schistocerca gregaria* as a model for reevaluating some current (neuro)endocrine concepts. *J. Insect Physiol.* 56:919–25
28. Defernez M, Kemsley EK. 1997. The use and misuse of chemometrics for treating classification problems. *Trends Anal. Chem.* 16:216–21
29. DeFries R. 2008. Terrestrial vegetation in the coupled human-earth system: contributions of remote sensing. *Annu. Rev. Environ. Resour.* 33:369–90
30. Dianguirard M, Slater PN. 1999. Calibration of space-multispectral imaging sensors: a review. *Remote Sens. Environ.* 68:194–205
31. Dickinson M, Farman G, Frye M, Bekyarova T, Gore D, et al. 2005. Molecular dynamics of cyclically contracting insect flight muscle in vivo. *Nature* 433:330–34

32. Dopido I, Zortea M, Villa A, Plaza A, Gamba P. 2011. Unmixing prior to supervised classification of remotely sensed hyperspectral images. *IEEE Geosci. Remote Sens. Lett.* 8:760–64
33. Dowell FE, Throne JE, Wang D, Baker JE. 1999. Identifying stored-grain insects using near-infrared spectroscopy. *J. Econ. Entomol.* 92:165–69
34. Dunagan SC, Gilmore MS, Varekamp JC. 2007. Effects of mercury on visible/near-infrared reflectance spectra of mustard spinach plants (*Brassica rapa* P.). *Environ. Pollut.* 148:301–11
35. Ehlers M, Klonus S, Johan PA, Rosso P. 2010. Multi-sensor image fusion for pansharpening in remote sensing. *Int. J. Image Data Fusion* 1:25–45
36. Eklundh L, Johansson T, Solberg S. 2009. Mapping insect defoliation in Scots pine with MODIS time-series data. *Remote Sens. Environ.* 113:1566–73
37. Faria FA, Perre P, Zucchi RA, Jorge LR, Lewinsohn TM, et al. 2014. Automatic identification of fruit flies (Diptera: Tephritidae). *J. Vis. Commun. Image Represent.* 25:1516–27
38. Ferreira-Caliman MJ, Nascimento FS, Turatti IC, Mateus S, Lopes NP, Zucchi R. 2010. The cuticular hydrocarbons profiles in the stingless bee *Melipona marginata* reflect task-related differences. *J. Insect Physiol.* 56:800–4
39. Floreano D, Wood RJ. 2015. Science, technology and the future of small autonomous drones. *Nature* 521:460–66
40. Geiselhardt S, Otte T, Hilker M. 2009. The role of cuticular hydrocarbons in male mating behavior of the mustard leaf beetle, *Phaedon cochleariae* (F.). *J. Chem. Ecol.* 35:1162–71
41. Gitelson A, Merzlyak MN. 1994. Spectral reflectance changes associated with autumn senescence of *Aesculus hippocastanum* L. and *Acer platanoides* L. leaves. Spectral features and relation to chlorophyll estimation. *J. Plant Physiol.* 143:286–92
42. Gowen AA, Marini F, Esquerre C, O'Donnell C, Downey G, Burger J. 2011. Time series hyperspectral chemical imaging data: challenges, solutions and applications. *Anal. Chim. Acta* 705:272–82
43. Guo B, Gunn SR, Damper RI, Nelson JDB. 2008. Customizing kernel functions for SVM-based hyperspectral image classification. *IEEE Trans. Geosci. Remote Sens.* 17:622–29
44. Ha W, Gowda PH, Howell TA. 2013. A review of downscaling methods for remote sensing-based irrigation management: part I. *Irrig. Sci.* 31:831–50
45. Hawkins DM. 2004. The problem of overfitting. *J. Chem. Inf. Comput. Sci.* 1:1–12
46. Honkavaara E, Arbiol R, Markelin L, Martinez L, Cramer M, et al. 2009. Digital airborne photogrammetry—a new tool for quantitative remote sensing? A state-of-the-art review on radiometric aspects of digital photogrammetric images. *Remote Sens.* 1:577–605
47. Horler DNH, Dockray M, Barber J, Barringer AR. 1983. Red edge measurements for remotely sensing plant chlorophyll content. *Adv. Space Res.* 3:273–77
48. Houle D, Govindaraju DR, Omholt S. 2010. Phenomics: the next challenge. *Nat. Rev. Genet.* 11:855–66
49. Howard RW, Baker JE. 2003. Cuticular hydrocarbons and wax esters of the ectoparasitoid *Habrobracon hebetor*: ontogenetic, reproductive, and nutritional effects. *Arch. Insect Biochem. Physiol.* 53:1–18
50. Howard RW, Blomquist GJ. 2005. Ecological, behavioral, and biochemical aspects of insect hydrocarbons. *Annu. Rev. Entomol.* 50:371–93
51. Howard RW, Pérez-Lachaud G. 2002. Cuticular hydrocarbons of the ectoparasitic wasp *Cephalonomia hyalinipennis* (Hymenoptera: Bethylidae) and its alternative host, the stored product pest *Caulophilus oryzae* (Coleoptera: Curculionidae). *Arch. Insect Biochem. Physiol.* 50:75–84
52. Huang F, Leonard BR, Moore SH, Cook DR, Baldwin J, et al. 2008. Allele frequency of resistance to *Bacillus thuringiensis* Cry1Ab corn in Louisiana populations of sugarcane borer (Lepidoptera: Crambidae). *J. Econ. Entomol.* 101:492–98
53. Huang J, Liao H, Zhu Y, Sun J, Sun Q, Liu X. 2012. Hyperspectral detection of rice damaged by rice leaf folder (*Cnaphalocrocis medinalis*). *Comput. Electron. Agric.* 82:100–7
54. Huang Y, Lan Y, Westbrook JK, Hoffmann WC. 2008. Remote sensing and GIS applications for precision area-wide pest management: implications for Homeland Security. In *Geospatial Technologies and Homeland Security*, ed. DZ Sui, 94:241–55. Dordrecht, Neth.: Springer
55. Iordache MD, Bioucas-Dias JM, Plaza A. 2011. Sparse unmixing of hyperspectral data. *IEEE Trans. Geosci. Remote Sens.* 49:2014–39

56. Irving TC, Maughan DW. 2000. In vivo X-ray diffraction of indirect flight muscle from *Drosophila melanogaster*. *Biophys. J.* 78:2511–15
57. Isaaks EH, Srivastava RM. 1989. *Applied Geostatistics*. New York: Oxford Univ. Press
58. Jean-Philippe S, Labbé N, Damay J, Franklin J, Hughes K. 2012. Effect of mercuric compounds on pine and sycamore germination and early survival. *Am. J. Plant Sci.* 3:150–58
59. Jia F, Magghirang E, Dowell F, Abel C, Ramaswamy S. 2007. Differentiating tobacco budworm and corn earworm using near-infrared spectroscopy. *J. Econ. Entomol.* 100:759–64
60. Joseph G. 2005. *Fundamentals of Remote Sensing*. Hyderabad, India: Universities Press
61. Kelly M, Guo Q. 2007. Integrated agricultural pest management through remote sensing and spatial analyses. In *General Concepts in Integrated Pest and Disease Management*, ed. A Ciancio, KG Mukerji, 1:191–207. Dordrecht, Neth.: Springer
62. Kemsley EK. 1996. Discriminant analysis of high-dimensional data: a comparison of principal components analysis and partial least squares data reduction methods. *Chemom. Intell. Lab. Syst.* 33:47–61
63. Klarica J, Bittner L, Pallua J, Pezzei C, Huck-Pezzei V, et al. 2011. Near-infrared imaging spectroscopy as a tool to discriminate two cryptic *Tetramorium* ant species. *J. Chem. Ecol.* 37:549–52
64. Korie S, Perry JN, Mugglestone MA, Clark SJ, Thomas CFG, Roff MN. 2000. Spatio-temporal associations in beetle and virus count data. *J. Agric. Biol. Environ. Stat.* 5:214–39
65. Kruse FA, Taranik JV, Coolbaugh M, Michaels J, Littlefield EF, et al. 2011. Effect of reduced spatial resolution on mineral mapping using imaging spectrometry—examples using hyperspectral infrared imager (HyspIRI)-simulated data. *Remote Sens.* 3:1584–602
66. Lacoste C, Nansen C, Thompson S, Moir-Barnetson L, Mian A, et al. 2015. Increased susceptibility to aphids of flowering wheat plants exposed to low temperatures. *Environ. Entomol.* 44:610–18
67. Laliberte AS, Goforth MA, Steele CM, Rango A. 2011. Multispectral remote sensing from unmanned aircraft: image processing workflows and applications for rangeland environments. *Remote Sens.* 3:2529–51
68. Lammertyn J, Peirs A, de Baerdemaeker J, Nicolaı B. 2000. Light penetration properties of NIR radiation in fruit with respect to non-destructive quality assessment. *Postharvest Biol. Technol.* 18:121–32
69. Land MF, Horwood J, Lim MLM, Li D. 2007. Optics of the ultraviolet reflecting scales of a jumping spider. *Proc. R. Soc. B* 274:1583–89
70. Lapointe SL, Hunter WB, Alessandro RT. 2004. Cuticular hydrocarbons on elytra of the *Diaprepes* root weevil *Diaprepes abbreviatus* (L.) (Coleoptera: Curculionidae). *Agric. Forest Entomol.* 6:251–57
71. Lee WS, Alchanatis V, Yang C, Hirafuji M, Moshoue D, Li C. 2010. Sensing technologies for precision specialty crop production. *Comput. Electron. Agric.* 74:2–33
72. Lefsky MA, Cohen WB, Parker GG, Harding DJ. 2002. Lidar remote sensing for ecosystem studies. *Bioscience* 52:19–30
73. Lei W, Huaguo H, Youqing L. 2010. *Remote sensing of insect pests in larch forest based on physical model*. Presented at Proc. Geosci. Remote Sens. Symp. (IGARSS), IEEE Int., July 25–30, Honolulu, HI
74. Lévesque J, King DJ. 2003. Spatial analysis of radiometric fractions from high-resolution multispectral imagery for modelling individual tree crown and forest canopy structure and health. *Remote Sens. Environ.* 84:589–602
75. Liebhold AM, Rossi RE, Kemp WP. 1993. Geostatistics and geographic information systems in applied insect ecology. *Annu. Rev. Entomol.* 38:303–27
76. Lim MLM, Land MF, Li D. 2007. Sex-specific UV and fluorescence function as courtship signals in jumping spiders. *Science* 315:481
77. Lu H, Zheng H, Hu Y, Lou H, Kong X. 2011. Bruise detection on red bayberry (*Myrica rubra* Sieb. & Zucc.) using fractal analysis and support vector machine. *J. Food Eng.* 104:149–53
78. Luo C, Wei C, Nansen C. 2015. How do “mute” cicadas produce their calling songs? *PLOS ONE* 10:e0118554
79. Luo J, Huang W, Yuan L, Zhao C, Du S, et al. 2013. Evaluation of spectral indices and continuous wavelet analysis to quantify aphid infestation in wheat. *Precis. Agric.* 14:151–61
80. Manickavasagan A, Jayas DS, White NDG. 2008. Thermal imaging to detect infestation by *Cryptolestes ferrugineus* inside wheat kernels. *J. Stored Prod. Res.* 44:186–92

81. Mantuano A, Pickler A, Barroso RC, de Almeida AP, Braz D, et al. 2012. Elemental changes in hemolymph and urine of *Rhodnius prolixus* induced by in-vivo exposure to mercury: a study using synchrotron radiation total reflection X-ray fluorescence. *Spectrochim. Acta B* 71–72:127–30
82. Markelin L, Honkavaara E, Peltoniemi J, Ahokas E, Kuittinen R, et al. 2008. Radiometric calibration and characterization of large-format digital photogrammetric sensors in a test field. *Photogramm. Eng. Remote Sens.* 74:1487–500
83. Mietchen D, Keupp H, Manz B, Volke F. 2005. Non-invasive diagnostics in fossils—magnetic resonance imaging of pathological belemnites. *Biogeosciences* 2:133–40
84. Mietchen D, Manz B, Volke F, Storey K. 2008. Assessment of cold adaptation in insect larvae by magnetic resonance imaging and magnetic resonance spectroscopy. *PLOS ONE* 3:e3826
85. Mirik M, Ansley RJ, Michels JGJ, Elliott NC. 2012. Spectral vegetation indices selected for quantifying Russian wheat aphid (*Diuraphis noxia*) feeding damage in wheat (*Triticum aestivum* L.). *Precis. Agric.* 13:501–16
86. Mirik M, Michels GJ, Kassymzhanova-Mirik S, Elliott NC, Bowling R. 2006. Hyperspectral spectrometry as a means to differentiate uninfested and infested winter wheat by greenbug (Hemiptera: Aphididae). *J. Econ. Entomol.* 99:1682–90
87. Mogren CL, Webb SM, Walton WE, Trumble JT. 2013. Micro X-ray absorption spectroscopic analysis of arsenic localization and biotransformation in *Chironomus riparius* Meigen (Diptera: Chironomidae) and *Culex tarsalis* Coquillett (Culicidae). *Environ. Pollut.* 180:78–83
88. Müller J, Brandl R. 2009. Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages. *J. Appl. Ecol.* 46:897–905
89. Muñoz-Huerta R, Guevara-Gonzalez R, Contreras-Medina L, Torres-Pacheco I, Prado-Olivarez J, Ocampo-Velazquez R. 2013. A review of methods for sensing the nitrogen status in plants: advantages, disadvantages and recent advances. *Sensors* 13:10823–43
90. Nansen C. 2011. Robustness of analyses of imaging data. *Opt. Express* 19:15173–80
91. Nansen C. 2012. Use of variogram parameters in analysis of hyperspectral imaging data acquired from dual-stressed crop leaves. *Remote Sens.* 4:180–93
92. Nansen C, Abidi N, Sidumo AJ, Gharalari AH. 2010. Using spatial structure analysis of hyperspectral imaging data and Fourier transformed infrared analysis to determine bioactivity of surface pesticide treatment. *Remote Sens.* 2:908–25
93. Nansen C, Coelho AJ, Mendes JV, Parra JRP. 2014. Reflectance-based identification of parasitized host eggs and adult *Trichogramma* specimens. *J. Exp. Biol.* 217:1187–92
94. Nansen C, Geremias LD, Xue Y, Huang F, Parra JR. 2013. Agricultural case studies of classification accuracy, spectral resolution, and model over-fitting. *Appl. Spectrosc.* 67:1332–38
95. Nansen C, Macedo T, Swanson R, Weaver DK. 2009. Use of spatial structure analysis of hyperspectral data cubes for detection of insect-induced stress in wheat plants. *Int. J. Remote Sens.* 30:2447–64
96. Nansen C, Ribeiro LP, Dadour I, Roberts JD. 2015. Detection of temporal changes in insect body reflectance in response to killing agents. *PLOS ONE* doi: 10.1371/journal.pone.0124866
97. Nansen C, Sidumo AJ, Capareda S. 2010. Variogram analysis of hyperspectral data analysis to characterize impact of biotic and abiotic stress of maize plants and to estimate biofuel potential. *Appl. Spectrosc.* 64:627–36
98. Nansen C, Sidumo AJ, Martini X, Stefanova K, Roberts JD. 2013. Reflectance-based assessment of spider mite “bio-response” to maize leaves and plant potassium content in different irrigation regimes. *Comput. Electron. Agric.* 97:21–26
99. Nansen C, Weaver DK, Sing SE, Runyon JB, Morrill WL, et al. 2005. Within-field spatial distribution of *Cephus cinctus* (Hymenoptera: Cephidae) larvae in Montana wheat fields. *Can. Entomol.* 137:202–14
100. Nansen C, Zhang X, Aryamanesh N, Yan G. 2014. Use of variogram analysis to classify field peas with and without internal defects caused by weevil infestation. *J. Food Eng.* 123:17–22
101. Newey P, Robson SKA, Crozier RH. 2009. Nest and colony-specific spectra in the weaver ant *Oecophylla smaragdina*. *Insectes Soc.* 56:261–68
102. Newey PS, Robson SKA, Crozier RH. 2008. Near-infrared spectroscopy as a tool in behavioural ecology: a case study of the weaver ant, *Oecophylla smaragdina*. *Anim. Behav.* 76:1727–33

103. Nguyen CV, Lovell DR, Adcock M, La Salle J. 2014. Capturing natural-colour 3D models of insects for species discovery and diagnostics. *PLOS ONE* 9:e94346
104. Nunes TM, Turatti ICC, Mateus S, Nascimento FS, Lopes NP, Zucchi R. 2009. Cuticular hydrocarbons in the stingless bee *Schwarziana quadripunctata* (Hymenoptera, Apidae, Meliponini): differences between colonies, castes and age. *Genet. Mol. Res.* 8:589–95
105. Patterson MCL, Brescia A. 2010. Operation of small sensor payloads on tactical sized unmanned air vehicles. *Aeronaut. J.* 114:427–36
106. Peddle DR, Hall FG, LeDrew EF. 1999. Spectral mixture analysis and geometric-optical reflectance modeling of boreal forest biophysical structure. *Remote Sens. Environ.* 67:288–97
107. Peleg K, Anderson GL, Yang C. 2005. Repeatability of hyperspectral imaging systems: quantification and improvement. *Int. J. Remote Sens.* 26:115–39
108. Perrings C, Dehnen-Schmutz K, Touza J, Williamson M. 2005. How to manage biological invasions under globalization. *Trends Ecol. Evol.* 20:212–15
109. Pimentel D, Zuniga R, Morrison D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol. Econ.* 52:273–88
110. Pinter PJ, Hatfield JL, Schepers JS, Barnes EM, Moran MS, et al. 2003. Remote sensing for crop management. *Photogramm. Eng. Remote Sens.* 69:647–64
111. Prabhakar M, Prasad YG, Rao MN. 2012. Remote sensing of biotic stress in crop plants and its applications for pest management. In *Crop Stress and Its Management: Perspectives and Strategies*, ed. B Venkateswarlu, AK Shanker, C Shanker, M Maheswari, pp. 517–49. New York: Springer
112. Qin J, Lu R. 2008. Measurement of the optical properties of fruits and vegetables using spatially resolved hyperspectral diffuse reflectance imaging technique. *Postharvest Biol. Technol.* 49:355–65
113. Raven PH, Evert RF, Eichorn SE. 1986. *Biology of Plants*. New York: Worth
114. Reeves WK, Peiris KHS, Scholte E-J, Wirtz RA, Dowell FE. 2010. Age-grading the biting midge *Culicoides sonorensis* using near-infrared spectroscopy. *Med. Vet. Entomol.* 24:32–37
115. Reisig DD, Godfrey LD. 2010. Remotely sensing arthropod and nutrient stressed plants: a case study with nitrogen and cotton aphid (Hemiptera: Aphididae). *Environ. Entomol.* 39:1255–63
116. Riedell WE, Blackmer TM. 1999. Leaf reflectance spectra of cereal aphid-damaged wheat. *Crop Sci.* 39:1835–40
117. Riley JR. 1989. Remote sensing in entomology. *Annu. Rev. Entomol.* 34:247–71
118. Riley JR, Xia-Nian C, Xiao-Xi Z, Reynolds DR, Guo-Min XU, et al. 1991. The long-distance migration of *Nilaparvata lugens* (Stål) (Delphacidae) in China: radar observations of mass return flight in the autumn. *Ecol. Entomol.* 16:471–89
119. Roux O, Gers C, Legal L. 2008. Ontogenetic study of three Calliphoridae of forensic importance through cuticular hydrocarbon analysis. *Med. Vet. Entomol.* 22:309–17
120. Royle DD, Lathrop RG. 2002. Discriminating *Tsuga canadensis* hemlock forest defoliation using remotely sensed change detection. *J. Nematol.* 34:213–21
121. Schotzko DJ, Quisenberry SS. 1999. Pea leaf weevil (Coleoptera: Curculionidae) spatial distribution in peas. *Environ. Entomol.* 28:477–84
122. Sikulu M, Killeen GF, Hugo LE, Ryan PA, Dowell KM, et al. 2010. Short report near-infrared spectroscopy as a complementary age grading and species identification tool for African malaria vectors. *Parasites Vectors* 3:1–7
123. Sikulu MT, Majambere S, Khatib BO, Ali AS, Hugo LE, Dowell FE. 2014. Using a near-infrared spectrometer to estimate the age of *Anopheles* mosquitoes exposed to pyrethroids. *PLOS ONE* 9:1–6
124. Simonett DS. 1983. *Manual of Remote Sensing*. Falls Church, VA: Am. Soc. Photogramm
125. Singh CB, Jayas DS, Paliwal J, White NDG. 2009. Detection of insect-damaged wheat kernels using near-infrared hyperspectral imaging. *J. Stored Prod. Res.* 45:151–58
126. Singh CB, Jayas DS, Paliwal J, White NDG. 2010. Identification of insect-damaged wheat kernels using short-wave near-infrared hyperspectral and digital colour imaging. *Comput. Electron. Agric.* 73:118–25
127. Smith AD, Reynolds DR, Riley JR. 2000. The use of vertical-looking radar to continuously monitor the insect fauna flying at altitude over southern England. *Bull. Entomol. Res.* 90:265–77
128. Stavrakoudis D, Dragozi E, Gitas I, Karydas C. 2014. Decision fusion based on hyperspectral and multispectral satellite imagery for accurate forest species mapping. *Remote Sens.* 6:6897–928

129. Steiner S, Mumm R, Ruther J. 2007. Courtship pheromones in parasitic wasps: comparison of bioactive and inactive hydrocarbon profiles by multivariate statistical methods. *J. Chem. Ecol.* 33:825–38
130. Stone C, Coops NC. 2004. Assessment and monitoring of damage from insects in Australian eucalypt forests and commercial plantations. *Aust. J. Entomol.* 43:283–92
131. Sudbrink DL, Harris FA, Robbins JT, English PJ, Willers JL. 2003. Evaluation of remote sensing to identify variability in cotton plant growth and correlation with larval densities of beet armyworm and cabbage looper (Lepidoptera: Noctuidae). *Fla. Entomol.* 86:290–94
132. Taylor LR. 1984. Assessing and interpreting the spatial distributions of insect populations. *Annu. Rev. Entomol.* 29:321–57
133. Thorp KR, Tian LF. 2004. A review on remote sensing of weeds in agriculture. *Precis. Agric.* 5:477–508
134. Trumble JT, Kolodny-Hirsch DM, Ting IP. 1993. Plant compensation for arthropod herbivory. *Annu. Rev. Entomol.* 38:93–119
135. Tueller PT. 1982. Remote sensing for range management. In *Remote Sensing in Resource Management*, ed. CJ Johannsen, JL Sanders, pp. 125–40. Ankeny, IN: Soil Conserv. Soc. Am.
136. Vadivambal R, Jayas DS. 2011. Applications of thermal imaging in agriculture and food industry—a review. *Food Bioprocess Technol.* 4:186–99
137. Villa A, Chanussot J, Benediktsson JA, Jutten C. 2011. Spectral unmixing for the classification of hyperspectral images at a finer spatial resolution. *IEEE J. Sel. Top. Signal Process.* 5:521–33
138. Wakabayashi K, Tokunaga M, Kohno I. 1992. Small-angle synchrotron X-ray scattering reveals distinct shape changes of the myosin head during hydrolysis of ATP. *Science* 258:443–47
139. Wang J, Nakano K, Ohashi S. 2011. Non-destructive detection of internal insect infestation in jujubes using visible and near-infrared spectroscopy. *Postharvest Biol. Technol.* 59:272–79
140. Wang J, Nakano K, Ohashi S, Takizawa K, He JG. 2010. Comparison of different modes of visible and near-infrared spectroscopy for detecting internal insect infestation in jujubes. *J. Food Eng.* 101:78–84
141. Wang Y, Nansen C, Zhang Y. 2015. Integrative insect taxonomy based on morphology, mitochondrial DNA and hyperspectral reflectance profiling. *Zool. J. Linn. Soc.* In press
142. Webster TC, Dowell FE, Maghirang EB, Thacker EM. 2009. Visible and near-infrared spectroscopy detects queen honey bee insemination. *Apidologie* 40:565–69
143. Westneat MW, Socha JJ, Lee WK. 2008. Advances in biological structure, function, and physiology using synchrotron X-ray imaging. *Annu. Rev. Physiol.* 70:119–42
144. Willers JL, Jenkins JN, Ladner WL, Gerard PD, Boykin DL, et al. 2005. Site-specific approaches to cotton insect control. sampling and remote sensing analysis techniques. *Precis. Agric.* 6:431–52
145. Wilson BC, Jacques SL. 1990. Optical reflectance and transmittance of tissues: principles and applications. *IEEE J. Quantum Electron.* 26:2186–99
146. Winder L, Perry JN, Holland JM. 1999. The spatial and temporal distribution of the grain aphid *Sitobion avenae* in winter wheat. *Entomol. Exp. Appl.* 93:277–90
147. Xie Y, Sha Z, Yu M. 2008. Remote sensing imagery in vegetation mapping: a review. *J. Plant Ecol.* 1:9–23
148. Yang C, Everitt JH, Bradford JM, Murden D. 2009. Comparison of airborne multispectral and hyperspectral imagery for estimating grain sorghum yield. *Trans. ASABE* 52:641–49
149. Yang C, Everitt JH, Fernandez CJ. 2010. Comparison of airborne multispectral and hyperspectral imagery for mapping cotton root rot. *Biosyst. Eng.* 107:131–39
150. Yang Z, Rao MN, Elliott NC, Kindler SD, Popham TW. 2005. Using ground-based multispectral radiometry to detect stress in wheat caused by greenbug (Homoptera: Aphididae) infestation. *Comput. Electron. Agric.* 47:121–35
151. Yang Z, Rao MN, Elliott NC, Kindler SD, Popham TW. 2009. Differentiating stress induced by greenbugs and Russian wheat aphids in wheat using remote sensing. *Comput. Electron. Agric.* 67:64–70
152. Yang Z, Rao MN, Kindler SD, Elliott NC. 2004. Remote sensing to detect plant stress, with particular reference to stress caused by the greenbug: a review. *Southwest. Entomol.* 29:227–36
153. Yeh C. 1994. *Applied Photonics*. San Diego, CA: Academic
154. Young AM. 1971. Wing coloration and reflectance in *Morpho* butterflies as related to reproductive behavior and escape from avian predators. *Oecologia* (*Berlin*) 7:209–22
155. Young T. 1807. *A Course of Lectures on Natural Philosophy and the Mechanical Arts*. London: Johnson

156. Zhang C, Kovacs JM. 2012. The application of small unmanned aerial systems for precision agriculture: a review. *Precis. Agric.* 13:693–712
157. Zhang C, Walters D, Kovacs JM. 2014. Applications of low altitude remote sensing in agriculture upon farmers' requests—a case study in northeastern Ontario, Canada. *PLOS ONE* 9:e112894
158. Zhang X, Nansen C, Aryamanesh N, Yan G, Boussaid F. 2015. Importance of spatial and spectral data reduction in detection of internal defects in food products. *Appl. Spectrosc.* 69:473–80
159. Zhu GH, Ye GY, Hu C, Xu XH, Li K. 2006. Development changes of cuticular hydrocarbons in *Chrysomya rufifacies* larvae: potential for determining larval age. *Med. Vet. Entomol.* 20:438–44
160. Zhu Y, Yao X, Tian Y, Liu X, Cao W. 2008. Analysis of common canopy vegetation indices for indicating leaf nitrogen accumulations in wheat and rice. *Int. J. Appl. Earth Obs. Geoinf.* 10:1–10
161. Zschokke S. 2002. Ultraviolet reflectance of spiders and their webs. *J. Arachnol.* 30:246–54