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Review Article

Abundance of *Sesamia nonagrioides* (Lef.) (Lepidoptera: Noctuidae) on the Edges of the Mediterranean Basin

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Organisms inhabiting seasonal environments are able to synchronize their life cycles with seasonal cycles of biotic and abiotic factors. Diapause, a state of low metabolic activity and developmental arrest, is used by many insect species to cope with adverse conditions. *Sesamia nonagrioides* is a serious pest of corn in the Mediterranean regions and Central Africa. It is multivoltine, with two to four generations per year, that overwinters as mature larva in the northern of the Sahara desert. Our purpose was to compare the response of the *S. nonagrioides* populations occurring in the broader circum-Mediterranean area, with particular attention to the diapause period and the different numbers of generations per season. To this end, we tried to determine whether populations in the area differ in their response to photoperiod and whether we can foresee the number of generations in different areas. We present a model for predicting the occurrence of the critical photoperiod according to latitude and temperature and the spread of *S. nonagrioides* in the circum-Mediterranean countries. Responses of populations to short-day length suggest that the spread of the species is associated with a gradual loss of diapause in the southern areas, and that diapause incidence is positively correlated with latitude.

1. Introduction

1.1. Host Plants and Distribution. The corn stalk borer, *Sesamia nonagrioides,* is a polyphagous species with a fairly wide range of host plants, including corn, sorghum, millet, rice, sugar cane, grasses, melon, asparagus, palms, banana, and the ornamental plant *Strelitzia reginae* [1–9]. The population levels of this species, which has considerable potential to establish itself in an area and become abundant, may therefore depend on the abundance of these hosts.

The occurrence of *S. nonagrioides*, including *S. nonagrioides botanephaga,* has been reported in Portugal [10, 11], Spain [12–14], the Canary Islands [15], France [16–18], Italy [19], Greece [20, 21], Cyprus [22], Turkey [23, 24], Morocco [25], Israel [26], Iran [27–29], Syria [30], Ethiopia [6], Ghana [31], and several other African countries [32]. *S. nonagrioides* has been considered the most important pest of maize in Spain since 1929 [12]. Nye [33] observed that *S. nonagrioides* was morphologically very close to one of the new sub-Saharan species that had been described (*Sesamia botanephaga*) and indicated that *Sesamia nonagrioides nonagrioides* and *Sesamia nonagrioides botanephaga* should be regarded as two subspecies distributed to the north and south of the Sahara, respectively. Esfandiari et al. [34] stated that African *S. botanephaga* (or *S. nonagrioides botanephaga*) do not occur in Iran and that it seems that *S. nonagrioides* is native to SW Iran rather than an exotic pest, having adopted sugarcane as a host after it began to be cultivated there about 70 years ago. Leyenaar and Hunter [31] reported that *S. n. botanephaga* can cause 63% loss in maize yield in the coastal savanna of Ghana. In Kenya, *S. nonagrioides* has been commonly recovered in maize fields [35]. The same authors report that these species and other stem borers that are currently restricted to wild hosts may have the potential to shift to cultivated cereals in cases of serious habitat fragmentation. Moyal et al. [36] recently concluded that there is a single species of *S. nonagrioides* but with three different, isolated conspecific populations: one in East Africa, one in West Africa, and a Palearctic one in the circum-Mediterranean countries.

In the circum-Mediterranean countries, *S. nonagrioides* has been designated as the most important pest of corn. Many researchers have attempted to document the economic losses that it causes in Spain, but the results are not clear because the damage is not distinguishable from that caused by *Ostrinia nubilalis*. Arias and Alvez [37] indicated that damage caused by maize borers could range from 5% to 30% of the yield depending on the date of sowing and the cultural cycle of maize. In Greece, the existence of the species was first reported by Stavrakis [38]. The pest increased steadily in the 1980s as a result of the use of new single hybrids and improved culture practices [21]. This increase was followed by problems caused by *S. nonagrioides*, especially in the late-sown crop (sown in early July after the harvest of small cereals) [39]. According to a pilot survey in October 2005, the dominant pest in sweet sorghum, *Sorghum bicolor* (L.) Moench, was *S. nonagrioides* [40].

1.2. Number of Generations and Diapause. The number of generations is marginally governed by the onset of diapause at various latitudes and there are fewer generations in the northern region than in the southern one. Three to four generations are completed per year in Greece [39]. Stavrakis [38] reported that the pupation of the overwintering population in Greece takes place in April-May. It seems that the fourth generation is partial since some of the late progeny of the third generation will not make it through [39].

In Spain and Portugal, the borer completes 2 generations and a partial third one per year [37, 41, 42], with the third one having a low population size in northern Spain [43]. The existence of two generations, in May and July-August, has been reported in France [44]. In Israel, the borer is at least a bivoltine wetland species, flying in March to July and in October [45]. In Iran, it completes 4 generations during the active season, with a partial 5th generation in second plantings [46]. It has also been referred to as multivoltine, with three to four generations per year in southern Portugal [47] and three generations per year in the Izmir area of Turkey [48].

Diapause of this species has been studied extensively [20, 49–52]. Eizaguirre and Albajes [49] and Fantinou et al. [51] reported that larval diapause is induced by the length of photoperiod and that constant temperature modifies the diapause response curve from type III to type I. According to previous studies, the early induction of diapause can be explained by the limited tolerance of insects originating in the tropics to low temperatures, and it could be a mechanism enabling the insect to extend its range into northern regions. It seems that temperature plays a double role in the occurrence of a supplementary generation by increasing the developmental rate and delaying the onset of diapause. Gillyboeuf et al. [53] observed that survival of diapausing larvae at low temperature may be related to the microclimate of the overwintering site and not to their freeze tolerance capacity. However, they argue that the freezing tolerance of *S. nonagrioides* may be a factor favoring northern expansion.

Fantinou et al. [20] and Eizaguirre et al. [54] stated that photoperiods longer than 12:12 h (L : D) terminate diapause and that field-collected larvae complete diapause spontaneously. Under a temperature similar to the natural field temperatures, diapause terminates in approximately 4 months, ensuring that the larvae reach the middle of winter without pupation. When diapause terminates, temperatures in the field are very low and larvae go into quiescence, allowing them to survive and to synchronize their cycle with that of the host plant. The fact that the temperature thresholds for diapause and postdiapause development are 3 or 4 degrees lower than that for continuous development [20, 41] explains the phenological model of *S. nonagrioides* described by López et al. [41]. Moreover, Fantinou and Kagkou [55] reported that under natural conditions the increase in nighttime temperature in late winter and early spring could function as a signal eliciting diapause development. This is ecologically important because in temperate regions insects are exposed to daily photoperiods and thermoperiods in which the long nights coincide with low temperatures. The specific role of low temperature exposure in regulating diapause development is not entirely clear, beyond the fact that exposure to low temperatures is not a prerequisite for diapause termination in this species [20]. The intensity of cold stress reflected in the level of mortality occurring in larvae suggests that the northern boundary of the species' expansion is defined by low temperatures.

2. Key Aspects for the Existence of the Species

2.1. Latitude and Critical Photoperiod. Figure 1 shows the latitude lines of the Mediterranean basin countries. *S. nonagrioides* can be found in northern, mainly European, countries between 35° and 46° N and in southern countries, such as Morocco, Iran, Syria, and Israel, between 31° and 35° N. Spain is located between 36° and 43° N, whereas Greece is located between 35° and 41.5° N. In all the circum-Mediterranean countries where *S. nonagrioides* has been found, including Morocco, the species overwinters as diapausing larvae [2, 21, 44, 56], but there is no evidence of diapause in the populations of warmer and more southern countries. The Sahara desert probably delimits the populations of the borer that diapause in the north from those that complete development without diapause in the south. Masaki [57] suggested that variations in the incidence of diapause might be due to the varying threshold of external stimuli that trigger diapause. If an insect has an extremely low threshold, it will enter diapause in a very wide range of environmental conditions, whereas if its threshold is extremely high, the conditions which induce its diapause might be nonexistent in the ordinary range of environment. Between these extreme thresholds, there is an intergraded series of the reaction thresholds.

According to Eizaguirre and Albajes [49], under laboratory conditions the critical photoperiod (that which induces 50% diapause) is reduced from 13 h 52 min at 18°C to 13 h 15 min at 25°C; this means that a 1°C decrease in temperature corresponds to an increase in the critical photoperiod of about 5.3 minutes. This range of the critical photoperiod corresponds closely to the day length on 15 August in regions where *S. nonagrioides* diapauses. In these regions, the duration of the day on 15 August, from sunrise to

Figure 1: The latitude lines of the Mediterranean basin countries (from Google maps).

sunset, is graduated approximately from 13 h 18 min at 31° N to 13 h 57 at 43° N, an increase in day length of approximately 3.16 minutes for each degree of latitude increase (Figure 2).

Figure 2 shows the critical photoperiod for each latitude and temperature. In view of this, on 15 August in the northern regions of Europe, the longer photoperiods induce lower percentages of diapause, whilst the shorter ones occurring in southern Europe induce higher percentages. These results may seem contradictory, because in the northern regions *S. nonagrioides* larvae enter diapause earlier than in the southern regions, but the explanation could be that temperature has been reported to play a significant role in diapause induction [20, 50, 55, 58].

Estimation of the critical photoperiod by Eizaguirre and Albajes [49] allows us to design a model that could help to predict the occurrence of the critical photoperiod according to the latitude and the temperature in various countries (Figure 2). This model could help us to estimate the percentage of the live larvae of a generation that will be induced to diapause, the larval proportion that may develop towards adulthood, and therefore the trend of the population density of the next (last) generation.

Figure 3 shows the variation in the climate of 6 cities of the area where *S. nonagrioides* is distributed. The critical photoperiod arrival in these cities based on the data of Figure 2 corresponds to 27 August in Bordeaux, 6-7 September in Teheran, 20 August in Milan, 31 August in Zaragoza, 20 August in Athens, and 6 September in Marrakech. Therefore, the differences in the onset of the critical photoperiods in the various areas do not seem to be significant.

2.2. Freezing Days and Number of Generations Per Year. Although the differences in the critical photoperiod are not very obvious, greater differences can be observed in the range of prevailing temperatures in each region. Milan is the city with most days with a mean minimum temperature below −1°C, whereas Teheran is the city with most days with a mean minimum temperature above 10°C and a mean maximum temperature above 27°C, although temperatures below −1°C may occur on a few days each year. *S. nonagrioides* seems to be to some extent susceptible to high temperatures in summer [56] and the endophytic larval behavior may protect the species from the extreme temperatures of some regions.

Figures 2 and 3 provide data on the factors affecting the number of generations of *S. nonagrioides* in the different regions of the circum-Mediterranean countries. In Northern Italy, *S. nonagrioides* is not present because it is very susceptible to the low winter temperatures [13, 44, 56] and the short period of time with mean minimum temperatures above 10°C (close to the threshold temperatures for the pest [40, 59]). In contrast, in Iran the species completes 4 to 5 generations that can be attributed to the long period of time with prevailing mean minimum temperatures above 10°C (Figure 3) and to the delayed onset of the critical photoperiod in September (Figure 2). Generally, warmer temperatures tend to be associated with a higher number of generations of the insect. The number of generations in a region depends on the early appearance of the first generation derived from overwintering larvae. Galichet [44], Lopez et al. [60], and Fantinou et al. [20] demonstrated that diapause terminates by the end of February, so the occurrence of the first generation will depend on the prevailing temperatures throughout March, taking into account that the threshold temperatures for postdiapause development are lower than those for normal larval development [54]. Once the first generation has occurred, the accumulation of heat units, degree days, will determine the number of generations completed per season before the arrival of the photoperiod that initiates diapause. The degree days (DG) necessary for the completion of one generation in maize are 616 DG according to Hilal [61] and 730 DG according to López et al. [41]. The number of generations will also determine the population size of the pest of the last generation: the population density of the last generation of *S. nonagrioides* is usually higher than that of the previous one because the host crop is available [21, 35].

Latitude	August																														September														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	27	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
47	879	877	875	873	871	869	867	865	863	861	859	857	855	853	851	849	847	845	843	841	839	837	835	833	831	829	827	825	823	821	819	817	815	813	811	809	807	805	803	801	799	797	795	793	791	789
46	876	874	872	870	868	866	864	862	860	858	856	854	852	850	848	846	844	842	840	838	836	834	832	830	828	826	824	822	820	818	816	814	812	810	808	806	804	802	800	798	796	794	792	790	788	786
45	872	870	868	866	864	862	860	858	856	854	852	850	848	846	844	842	840	838	836	834	832	830	828	826	824	822	820	818	816	814	812	810	808	806	804	802	800	798	796	794	792	790	788	786	784	782
44	869	867	865	863	861	859	857	855	853	851	849	847	845	843	841	839	837	835	833	831	829	827	825	823	821	819	817	815	813	811	809	807	805	803	801	799	797	795	793	791	789	787	785	783	781	779
43	865	863	861	859	857	855	853	851	849	847	845	843	841	839	837	835	833	831	829	827	825	823	821	819	817	815	813	811	809	807	805	803	801	799	797	795	793	791	789	787	785	783	781	779	777	775
42	862	860	858	856	854	852	850	848	846	844	842	840	838	836	834	832	830	828	826	824	822	820	818	816	814	812	810	808	806	804	802	800	798	796	794	792	790	788	786	784	782	780	778	776	774	772
41	858	856	854	852	850	848	846	844	842	840	838	836	834	832	830	828	826	824	822	820	818	816	814	812	810	808	806	804	802	800	798	796	794	792	790	788	786	784	782	780	778	776	774	772	770	768
40	855	853	851	849	847	845	843	841	839	837	835	833	831	829	827	825	823	821	819	817	815	813	811	809	807	805	803	801	799	797	795	793	791	789	787	785	783	781	779	777	775	773	771	769	767	765
39	852	850	848	846	844	842	840	838	836	834	832	830	828	826	824	822	820	818	816	814	812	810	808	806	804	802	800	798	796	794	792	790	788	786	784	782	780	778	776	774	772	770	768	766	764	762
38	848	846	844	842	840	838	836	834	832	830	828	826	824	822	820	818	816	814	812	810	808	806	804	802	800	798	796	794	792	790	788	786	784	782	780	778	776	774	772	770	768	766	764	762	760	758
37	845	843	841	839	837	835	833	831	829	827	825	823	821	819	817	815	813	811	809	807	805	803	801	799	797	795	793	791	789	787	785	783	781	779	777	775	773	771	769	767	765	763	761	759	757	755
36	841	839	837	835	833	831	829	827	825	823	821	819	817	815	813	811	809	807	805	803	801	799	797	795	793	791	789	787	785	783	781	779	777	775	773	771	769	767	765	763	761	759	757	755	753	751
35	838	836	834	832	830	828	826	824	822	820	818	816	814	812	810	808	806	804	802	800	798	796	794	792	790	788	786	784	782	780	778	776	774	772	770	768	766	764	762	760	758	756	754	752	750	748
34	835	833	831	829	827	825	823	821	819	817	815	813	811	809	807	805	803	801	799	797	795	793	791	789	787	785	783	781	779	777	775	773	771	769	767	765	763	761	759	757	755	753	751	749	747	745

16°C
18°C
20°C
22°C
24°C
26°C
28°C

Figure 2: Variation in the length of the day, in minutes, from 1 August to 15 September according to latitude. Length of the day in color indicates the day of the critical photoperiod inducing 50% diapause for this temperature and latitude.

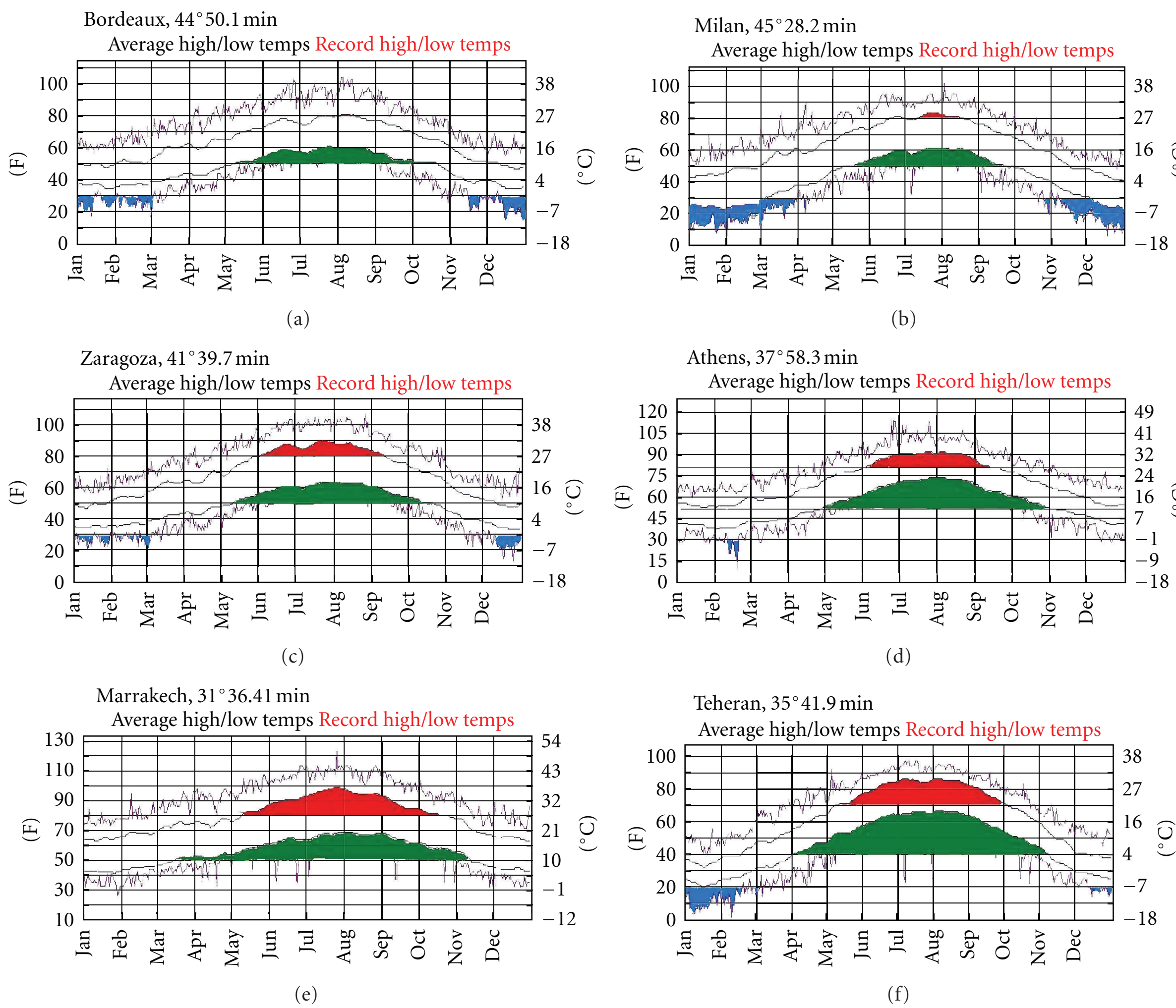

Figure 3: Maximum and minimum temperatures of six cities in the area of distribution of *Sesamia nonagrioides*. The curves, from bottom to top, show the record minimum temperatures, the mean minimum temperatures, the mean maximum temperatures, and the record maximum temperatures. Days with mean maximum temperatures higher than 27°C are colored in red, days with mean minimum temperatures higher than 10°C are colored in green, and days with temperatures below −1°C are colored in blue.

Consequently, like many multivoltine species that undergo a state of diapause, *S. nonagrioides* may complete as many generations as temperature and photoperiod conditions will allow, assuming that there is an available food source.

2.3. Winter Mortality. The overwinter mortality of *S. nonagrioides* in the Mediterranean is not only determined by the number of freezing days in winter but may also be associated with the percentage of the larval population that "escape" the critical photoperiod in autumn. If the weather remains warm, it is likely that many larvae will avoid diapause because of the high temperatures. Therefore, a further generation will lay eggs on a suitable green crop if it is available, and the neonate larvae will successfully develop only in those regions where relatively mild autumn temperatures can occur. However, the young larvae that are subsequently exposed to the later winter temperatures are destined to die. Therefore, the higher the percentage of larvae that escape from diapause during autumn, the higher the mortality of the next generation of young larvae.

3. Summary

Field populations of *S. nonagrioides* in the Mediterranean region display winter diapause. Voltinism in this species is a seasonally plastic trait dependent on early emergence of adults of the overwintering generation. The abundance of the species in a given region depends on the number of freezing days of the winter and the heat units accumulated from diapause termination until the arrival of the critical photoperiod for diapause induction in late summer. The species relies on latitudinal gradients in temperature and photoperiod for the induction of diapause, and the effect of environmental cues on diapause and adaptation to local environmental conditions is, therefore, variable.

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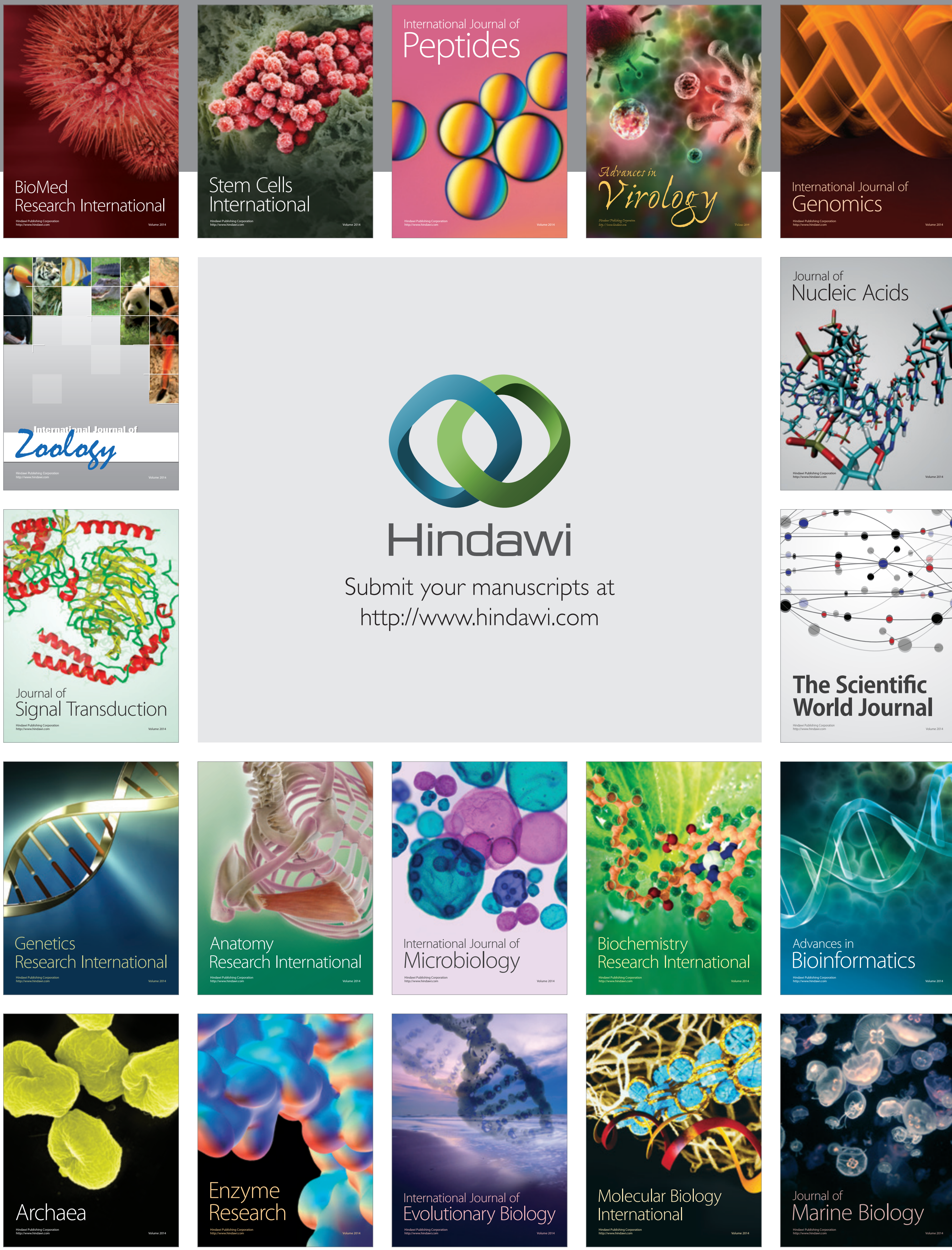
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