Current Trends in Natural Sciences (on-line) ISSN: 2284-953X ISSN-L: 2284-9521

THE THYSANOPTERA - *TRIFOLIUM REPENS* RELATIONSHIP IN A URBAN PARK OF ROMANIA

Daniela Bărbuceanu ^{1,*}, Liliana Vasiliu - Oromulu ²

¹University of Pitești, Faculty of Science, Physical Education and Informatics, Department of Natural Sciences, Târgu din Vale St. 1, 110040, Pitești, Romania ²Institute of Biology, Spl. Independentei 296, Bucharest, Romania

Abstract

Studies conducted in May-September 2015 in a park in Pitesti (Romania) highlighted the taxonomic and ecological structure of the thrips fauna on Trifolium repens. Specific diversity was provided by 13 species belonging to the two trophic levels: primary and secondary consumers. Eight species are mentioned for the first time on Trifolium in Romania, completing the list of taxa inhabiting the inflorescences of this plant. Frankliniella intonsa, xerophylous, polyphagous species, overwhelmingly dominates the populations of other species of thrips with 84.4%. During the dry and warm summer months, the mesophilous Haplothrips leucanthemi discreetly manifest its attachment towards this host plant, with relative abundances of up to 12.4%. The Shannon-Wiener diversity index and equitability register low values, due to unequal contribution of the thrips to the establishment of this coenosis. Air pollution by heavy metals due to heavy car traffic in this area leads to antennal anomalies of F. intonsa individuals, phenomenon encountered in Bucharest parks, too. Antennal anomalies occurring both in females and males confirm the role of air quality bioindicator played by the F. intonsa species. The results recommend the T. repens for monitoring thrips populations from areas subject to urban air pollution generated by heavy traffic.

Keywords: air pollution, antennal anomalies, biodiversity, park, Thysanoptera.

1. INTRODUCTION

In Europe *Trifolium repens* Linnaeus is a species of Fabaceae with an important contribution to the development of phytocoenoses of urban parks. This weed is common in ecosystems that have been subjected to studies on species of Thysanoptera. Thus, in Hungary, Jenser (1990) investigates the relationships between thrips and 12 species of fabacee from ecosystems surrounding forests, mentioning four species, on *T. repens*. In Croatia, in grassland ecosystems, Raspudić et al. (2009) identified eight species of Thysanoptera on this plant. In Romania, Knechtel (1951) and Knechtel et Vasiliu (1964) quotes eight species of Thysanoptera in inflorescences on *Trifolium* spp. collected from different geographical areas, of which only *Kakothrips robustus* (Uzel, 1895) and *Aptinothrips elegans* Priesner, 1924 species were reported specifically from *T. repens*. Vasiliu & Burlacu (1970), Vasiliu-Oromulu (2002a) mention *Aeolothrips intermedius* Bagnall 1934 and *Haplothrips leucanthemi* (Schrank 1781) (syn *H. niger* Osborn 1883) (Mound & Minaei, 2007) additionally from on this plant.

In a former study about air pollution in the parks of Bucharest Vasiliu-Oromulu & Bărbuceanu (2008) mention *H. leucanthemi* on a related plant, *T. pretense*.

Current Trends in Natural Sciences (on-line) ISSN: 2284-953X ISSN-L: 2284-9521

The purpose of this work is to investigate the importance of *T. repens* in city parks as trophic niche for Thysanoptera, and consequently in ensuring biodiversity in the urban space, as well as the impact air pollution road traffic has upon insects belonging to the Thysanoptera order.

2. MATERIALS AND METHODS

The observations were carried out during May-September 2015 on inflorescences of *T. repens* in Petrochimiştilor Park. The Park, with an area of about 14,000 sq m., is located in the southern part of Piteşti, when entering the town from the Piteşti-Bucureşti motorway (Romania), on the valley of the Geamăna River, the area being characterized by heavy traffic. The localization in System Stereo '70 is x=370053, 32 m and y=492985, 83 m.

In the weed vegetation *Trifolium repens* and *Lolium perenne* are dominant. Other rather commonly encountered spontaneous species are: *Ranunculus repens, Clematis vitalba, Geum urbanum, Potentilla argentea, P. reptans, Lotus corniculatus, Medicago lupulina, Trifolium pratense, Taraxacum officinale* and *Hordeum murinum.*

Some species are cultivated, such as: Pinus strobus, Taxus baccata, Juniperus horizontalis, Ligustrum vulgare.

For investigation of Thysanoptera, *T. repens* was selected by the facts that it has a long flowering period, a high dominancy and the small size, making it resistant to park maintenance activities. Monthly at random in the park 10 samplings each consisting of 10 inflorescences were made. Identification and counting of thrips from the inflorescences were made under a microscope using the keys Knechtel (1951), Schliephacke & Klimt (1979), Strassen (2003).

In order to assess the diversity of the ecosystem, the Shannon-Weaver diversity index was calculated, using the formula improved by Lloyd & Ghelardi (1964):

$$H(S) = \frac{K}{N} (N\log 10N - \sum_{p=1}^{S} Nr \log 10Nr) \text{ where:}$$

H = index; S = total number of species; K = 3, 321928; N = total number of individuals; Nr. = total number of individuals in species r. Immature thrips were not included in the count.

3. RESULTS AND DISCUSSIONS

Biodiversity

Researches have revealed a rich diversity of the thrips fauna on *T. repens* in a park, in terms of taxonomy, ecology and geographical distribution.

Taxonomically, those 1,765 adults and 211 larvae (Table 1) belong to two suborders, three families and 13 species.

Three of the identified species, *Aeolothrips intermedius, Frankliniella intonsa*, and *Thrips tabaci* are quoted by Raspudić et al. (2009) on *T. repens*, in Croatia, and *F. intonsa*, *T. tabaci* and *H. leucanthemi* are identified by Jenser (1990) in Hungary. Trophic diversity is ensured by affiliation to the two trophic levels, primary consumers, most of the species, and secondary, *Aeolothrips fasciatus*, and *A. intermedius*. The polyphagous nature of thrips species causes the *Trifolium* inflorescences to be inhabited under conditions of a poor trophic spectrum, situation specific to the urban area. Ecological diversity is supported by the presence in this small coenosis of both gramineous, floricolous and foliolous species, mesophilous and xerophilous ones. Typical floricolous species are dominant, two species are gramineous form, *Chirothrips manicatus*, and *Haplothrips aculeatus*.

Current	Trends	in	Natural	Sciences
---------	--------	----	---------	----------

Current Trends in Natural Sciences (on-line) ISSN: 2284-953X ISSN-L: 2284-9521 Current Trends in Natural Sciences (CD-Rom) ISSN: 2284-9521 ISSN-L: 2284-9521

Specific diversity at the geographical distribution level requires Euro-Siberian elements as dominant, a situation encountered in many of the Thysanoptera coenoses from other ecosystem types studied in Romania (Vasiliu-Oromulu, 1998).

Suborder	Family	Species	No. ind.	A (%)	Geographical distribution
	Aeolo-	Aeolothrips fasciatus (Linnaeus, 1758)	1₽	0.06	HOL
	thripidae	Aeolothrips intermedius Bagnall 1934	3 ♀♀	0.17	PAL
		Chirothrips manicatus Haliday 1836	1♀	0.06	HOL
		Frankliniella intonsa (Trybom 1895)	Trybom 1895) 1288♀♀;		EUS
			201 ් ්	84.4	EUS
	Thripidae	Frankliniella pallida Uzel, 1895	13♀♀; 2♂♂	0.85	EUR
Terebrantia		Odontothrips loti Haliday, 1852	1♀	0.06	HOL
		Thrips flavus Schrank, 1776	1₽	0.06	COS
		Thrips physapus Linnaeus, 1761	1₽	0.06	EUS
		Thrips tabaci (Lindeman, 1888)	31♀♀		COS
				1.76	
		Thrips validus Uzel, 1895	1₽	0.06	EUS
		F. intonsa larvae	195		
		Haplothrips aculeatus (Fabricius, 1803)	1₽	0.06	PAL
Tubuliford	Phlaeotripi-	Haplothrips leucanthemi (Schrank 1781)	219 ♀♀	12.4	EUS
Tubulliera	dae	Haplothrips setiger (Priesner, 1921)	19	0.06	WPAL
		H. leucanthemi larvae	16		-
		Total adults	1765		

Table	1.Specific	diversity of	Thysanoptera	fauna on	Trifolium	repens
-------	------------	--------------	--------------	----------	-----------	--------

COS=Cosmopolite; EUR= European; EUS=Euro-Siberian; HOL= Holarctic; PAL= Palaearctic; WPAL= West -Palaearctic.

Except for the two species of the genus *Frankliniella*, the other species were represented in our collections only by females (Table 1). Results of the most abundant species in this study, *F. intonsa*, shows a percentage of females of 84.4% and sex ratio of 0.15. In periods characterized by very high temperatures, females dominate significantly (Fig. 1).

In temperate areas, when autumn is near in some species of thrips a change of the sex ratio is obviously in favour of males (Mound, 1992).

Ecological indicators

Analysis of structural indicators shows important quantitative and qualitative differences in a temporal dynamics, with respect to the ecological requirements of each species.

F. intonsa and *H. leucanthemi* represent the nucleus of the Thysanoptera association, with the highest values of structural indicators (Table 1 and 2). These species are mentioned by Jenser (1990) on *T. repens*, *F. intonsa* with a relative abundance of 88%, and *H. leucanthemi* of only 6%, situation also reflected by our study.

Collections of May – September reveal a high specific diversity on this plant – under the conditions of a poor vegetal spectrum in parks – ranging between four and eight species, being lower in periods with high temperatures, namely June - July. However, except for the two species, *F. intonsa* and *H. leucanthemi*, the values of the structural indicators are minimal, their contribution to biomass of biocenosis being insignificant. Inhabiting the inflorescences and remarkable polyphagia of *F. intonsa* are highlighted in this study.

In May 2015, the Thysanoptera coenosis consists of five species, the populations of *F. intonsa* and *H. leucanthemi* having balanced contributions in valuing the trophic resources. The maximum values of constancy express the attachment of the two species towards this host plant. Characterized

Vol. 8, Issue 15, pp. 56-63, 2019

Current Trends in Natural Sciences (on-line) ISSN: 2284-953X ISSN-L: 2284-9521

95.5 94.25 100 88.52 90 80 70 57.43 56.41 60 50 42 56 40 30 20 10 May June July August Septembe ■ female min male

by a higher hydric regime, the month of May favours both qualitatively and quantitatively the mesophilous species, and equitability registers the highest value of all collections: 49.

Figure 1. Sex-ratio on Frankliniella intonsa species

The results of the samples of June 2015 highlights the xerophylous species *F. intonsa* as the most efficient in exploiting the trophic substrate, and ensuring the highest production of biomass throughout the period of study. Increasing temperatures during this month is also indicated by the appearance of another xerophylous species, *F. pallida*. The Shannon-Wiener diversity index is influenced by equitability which has the lowest value of all samples: 3.77.

In July, the taxonomic spectrum is the lowest one, only four species being hosted by *T. repens*. Unlike the previous month, *H. leucanthemi* reappears in samples, both as adults and larvae, and numerical abundances, although low, ensure its status of dominant species (6.53%), along with the inflorescence thrips (92.88%).

Regarding the collection of August 2015, the thrips coenosis belong to eight species, denoting the hightest specific richness. The species with the most important role in setting the coenosis remains the floricolous F. *intonsa* with a numerical abundance of 148 individuals which ensures a dominance of 83.62%.

In September, the last month of collecting, Thysanoptera association is composed of six species, F. *intonsa* being the one that values the trophic substrate at a rate of 82.11%. In this month *Thrips tabaci* shows to be present in higher numbers with a frequency of 60% in samples and a relative abundance of 10.53%.

In this study, the attachment of *F. intonsa* to the inflorescences of *T. repens* is also proved by the results of the study on the thrips fauna on inflorescences of *Matricaria chamomilla*, where *T. tabaci* and *H. leucanthemi* are the species with the highest values of the structural parameters, and *F. intonsa* has a sporadic presence (Bărbuceanu et al., 2013).

The presence of numerous *F. intonsa* and *H. leucanthemi* larvae on the white clover on all collection dates expresses the capacity of renewal of thrips populations in an ecosystem subject to permanent anthropogenic pressures.

Current Trends in Natural Sciences (on-line) ISSN: 2284-953X ISSN-L: 2284-9521

Current Trends in Natural Sciences (CD-Rom) ISSN: 2284-9521 ISSN-L: 2284-9521

i ubie 2. i ne shuclulul l		indicators of the thrips popula		uons on Injouum repens			1
May 21, 2015	No. individuals	Eroare! Obiectele nu se creează din editarea codurilor de câmp.	STDEV (standard deviation)	mg.wet matter/m ²	A%	C%	p _i log p _i
Aeolothrips intermedius	2	0.2	0.4	1.6	0.54	20	-0.012
Frankliniella intonsa	183	18.3	15	146.4	49.73	100	-0.151
Thrips tabaci	3	0.3	0.5	2.4	0.82	30	-0.017
Hanlothrins leucanthemi	179	17.9	12	143.2	48.64	100	-0.152
Haplothrips setiger	1	0.1	0.3	0.8	0,27	10	-0.007
Σ	368	36.8	21	294.4	100.00		-0.339
	H(S)	=1.12	Hmax	=2.0		E%	=49
<i>E. intonsa</i> larvae	8	H. leucanthemi lar	vae	4			
June 25, 2015				-			
Frankliniella intonsa	689	68.9	25.7	551.2	99.28	100	-0.003
Frankliniella pallida	1	0.1	0.3	0.8	0.14	10	-0.004
Thrips flavus	1	0.1	0.3	0.8	0.14	10	-0.004
Thrips fabaci	2	0.2	0.4	1.6	0.29	20	-0.007
Thrips validus	1	0.1	0.3	0.8	0.14	10	-0.004
S	694	69.4	25.6	555.2	100.00		-0.023
	H(S)	= 0.075	Hmax	= 2.322		E%	= 3.77
E intonsa larvao	102						
T. monsu fai vac							
A alathring intermedius	1	0.1	0.3	0.8	0.30	10	-0.008
Eventlinialla interna	313	31.3	19.0	250.4	92.88	100	-0.030
Frankliniella pallida	1	0.1	0.3	0.8	0.30	100	-0.008
Hanlothning laugantomi	22	2.2	3.7	17.6	6.53	30	-0.077
	337	3 37	17.5	269.6	100.00	20	-0.122
<u> </u>	H(S)	= 0.3156	Hmax	=2.0	100.00	E%	= 20.29
	56	0.0100	II laws and a		1	270	20.22
August 20, 2015			n. leucaninel	<i>mi</i> larvae	-		
August 29, 2013	1	0.1	0.3	0.8	0.56	10	-0.013
Engelinial a interna	148	14.8	8	118.4	83.62	100	-0.065
Frankliniella intonsa	8	0.8	13	64	4 52	40	-0.061
Odontothring loti	1	0.1	0.3	0.8	0.56	10	-0.013
Thring physerus	1	0.1	0.3	0.8	0.56	10	-0.013
Thrips tabaci	6	0.6	0.8	4.80	3.39	40	-0.050
Thrips under	1	0.1	0.3	0.8	0.56	10	-0.013
Hanlothring law and and	11	11	15	8.8	6.21	40	-0.075
riapioinrips ieucanthemi	177	17.7	9.1	141.6	100.00		-0 301
2	H(S)	- 1.00115	Hmax	-3.0	100.00	F%	-33
E interes la	10	- 1.00115		-5.0	10	L /0	_55
<i>F. intonsa</i> larvae	10		H. leucanthemi larvae		10		
September 21, 2015	1	0.1	0.3	0.8	0.53	10	_0.012
Chirothrips manicatus	1	15.6	0.3	1/2 2	0.55 87 11	10	-0.012
Frankliniella intonsa	150	0.5	0.7	143.2	2.62	40	-0.07
Frankliniella pallida	3	0.5	0.7	4	2.03	40	-0.042
Thrips tabaci	20	2.0	0.2	10.00	0.52	10	-0.105
Haplothrips aculeatus	1	0.1	0.3	0.8	0.53	10	-0.012

Table 2. The structural indicators of the thrips populations on Trifolium repens

Vol. 8, Issue 15, pp. 56-63, 2019

Current Trends in Natural Sciences (on-line) ISSN: 2284-953X ISSN-L: 2284-9521

Haplothrips leucanthemi	7	0.7	1.1	5.6	3.68	40	-0.053
Σ	190	19	10	170.4	100.00		-0.292
F. intonsa larvae - 19	H(S)	= 0.96868	Hmax	=3.0		E%	=37

Low values of constancy of most thrips species in relation to this host, the white clover, reflect a dynamic coenosis, these insects being extremely mobile, polyphagia also contributing to this behaviour.

F. intonsa, species with the highest values of structural indicators, has the highest contribution in the production of biomass within the coenosis.

Influence of urban air pollution on the Thysanoptera fauna on T. repens

Vasiliu-Oromulu et al. (2008), in a study on Thysanoptera fauna in Bucharest parks exposed to heavy metal pollution due to urban traffic (Pb, Cu, Zn, Cd) recorded morphological changes in F. *intonsa* species, manifested by different body discolorations and, especially, antennal anomalies. The authors consider F. *intonsa* species resistant, and in the same time sensitive to urban pollution. In addition to morphological changes it also presents high numerical abundance compared to other species.

F. intonsa registers such abundances also in our study, due to the contribution of polyphagous and xerophylous character of the species. A possible explanation of significant numerical abundances in May and September, to the detriment of the species typical for the white clover – mesophilous *H. leucanthemi*, might be the resistance manifested by *F. intonsa* towards pollution generated by cars traffic in this area. Air pollution is indicated by the presence of numerous individuals with antennal anomalies. Thus, our study revealed the presence of antennal anomalies in 11 females and one male of *F. intonsa* (Table 3).

It should be noted that such changes have not been observed in species from unpolluted grassland in mountains studies conducted to date (Vasiliu-Oromulu, 2002b).

Anomalies affected both the left and right antenna and consisted in shortening or lengthening certain articles, in reducing the number of antennas – most often or in the merger of two terminal articles (Fig. 2). It notices a constant distribution of these anomalies in all the period of studying.

Species	Date of collected	No. ind.	No. ind. with antennal anomalia		
			22/33	%	
	May	183	1	0.55	
Enauklini olla intonaa	June	689	6/1	1.01	
Frankliniella infonsa	July	313	1	0.32	
	August	148	1	0.67	
	September	156	2	1.38	
Total		1489	12	0.8	
Haplothrips leucanthemi	May	179	1	0.55	

Table 3. Anntenal anomalies to Thysanoptera species in Petrochimistilor Park, Pitesti, 2015

During observations, a *H. leucanthemi* female with left antennal anomaly was highlighted which constitutes a scientific novelty (Fig. 3).

Although the percentage of individuals with antennal anomalies is low, 0.32-1.38%, their constant presence demonstrates that in areas exposed to air pollution, life conditions for living organisms (plants, animals, and humans) are far from optimal.

Detailed studies will be required to cover the content in heavy metals at the level of soil, of the host plant *T. repens* and the thrips, *F. intonsa* and *H. leucanthemi*.

http://www.natsci.upit.ro

*Corresponding author, E-mail address: daniela barbuceanu@yahoo.com

Vol. 8, Issue 15, pp. 56-63, 2019

Current Trends in Natural Sciences (on-line) ISSN: 2284-953X ISSN-L: 2284-9521 Current Trends in Natural Sciences (CD-Rom) ISSN: 2284-9521 ISSN-L: 2284-9521



Figure 2. Frankliniella intonsa- a-d: antennal anomalies; f - normal antenna (original)



Figure 3. Haplothrips leucanthemi - a: antennal anomaly; b - normal antenna (original)

4. CONCLUSIONS

The values of ecological indicators confirm *T. repens* serves as a host plant for *F. intonsa* and *H. leucanthemi*. The xerophylous polyphagous *F. intonsa* dominates the populations of other species with relative abundance values ranging from 49.73% to 99.28% during temporal dynamics.

Species Aeolothrips fasciatus, Chirothrips manicatus, Frankliniella pallida, Odontothrips loti, Thrips physapus, T. validus, Haplothrips aculeatus, H. setiger are recorded for the first time on T. repens in our country and complete the list of taxa inhabiting this plant.

It is for the first time an antennal anomaly is shown in the species H. *leucanthemi*. Antennal anomalies occurring both in females and males confirm the role of air quality bioindicator played by the F. *intonsa*.

Despite air pollution and poor vegetal spectrum, this study highlights the fact that the parks can represent refuges for this group of insects, contributing to the conservation of its biodiversity.

5. ACKNOWLEDGEMENTS

Thanks to my colleagues Ph.D. Monica Neblea for identification of the plant communities, to Ph.D. Mădălina Marian for System Stereo '70 coordinates, and to Ph.D. Gijsbertus Vierbergen from Plant Protection Service Wageningen (Netherlands) for his helpful suggestions and corrections in preparating this paper.

Vol. 8, Issue 15, pp. 56-63, 2019

Current Trends in Natural Sciences (on-line) ISSN: 2284-953X ISSN-L: 2284-9521

6. REFERENCES

- Bărbuceanu, D., Vasiliu-Oromulu, L., Bărbuceanu, M. (2013). Matricaria chamomilla as trophic niche for thrips populations (Insecta: Thysanoptera). *Oltenia Journal for Studies in Natural Sciences*, 29 (1), 166-170.
- Jenser, G. (1990). Host preference of some Thysanoptera species living in Fabaceae flowers. In: *Proceed. 3rd Int. Symp. Thysanoptera*, Kazimircz Dolny, Poland, 83-89.
- Knechtel, W. K. (1951). Thysanoptera, Fauna R. P. România, Insecta. Vol. 8 (1). Edit. Academiei R. S. R. București. București.
- Knechtel, W. K., Vasiliu, L. (1964). Contribution à l'étude ecologique des Thysanoptères. *Rev. Roum. Biol., S. Zool.,* IX, 5, 355-363.
- Lewis, T. (1973). Thrips. Their biology, ecology and economic importance. Academic Press London and New York. London.
- Lloyd, M., Ghelardi, R., J. (1964). A table for calculating the equitability component of species diversity. J. Animal *Ecol.*, 33, 217-225.
- Mound, L. (1992). Patterns of sexuality in Thysanoptera. In E.A Cameron, et al., eds. The 1991 Conference on Thrips (Thysanoptera): Insect and Disease considerations in Sugar Maple Management (pp.2-14). U.S. Department of Agriculture, Forest Service, General Technical Report NE-161.
- Mound, L. A., Minaei, K. (2007). Australian thrips of the Haplothrips lineage (Insecta: Thysanoptera). *Journal of Natural History* 41, 2919–2978. Retrieved October 16, 2016, from http://www.tandfonline.com/doi/abs/10.1080/00222930701783219, doi: 10.1080/00222930701783219
- Raspudić, E., Ivezić, M., Brmež, M., Trdan, S. (2009). Distribution of Thysanoptera species and their host plants in Croatia. Acta agriculturae Slovenica, 93(3), 275-283. Retrieved January 18, 2016, from http://aas.bf.unilj.si/september2009/02raspudic.pdf.
- Schliephacke, G., Klimt, K. (1979). Thysanoptera, Fransenflügler. VEB Gustav Fischer Verlag. Jena.
- Strassen, R., Zur. (2003). Die terebranten Thysanopteren Europas und des Mittelmeer-Gebietes. Edit. Verlag Goecke & Evers. Keltern, Germany.
- Vasiliu, L., Burlacu, Gh. (1970). Influence of temperature upon energy metabolism in Aeolothrips intermedius Bagnall (Aelothripidae:Thysanoptera). *Rev. Rom., Biol-Zoologie*, Bucharest, 15 (5), 355-358.
- Vasiliu-Oromulu, L. (1998). The geographical distribution of Romanian Thysanoptera species (Insecta: Thysanoptera). *Entomologica Romanica*, 3, 67-72.
- Vasiliu-Oromulu, L. (2002a). The distribution of thrips species (Insecta:Thysanoptera) on different plants. *Entomologica Romanica*, 7, 17-24.
- Vasiliu-Oromulu, L. (2002b). The temporal and spatial dynamics of the thrips populations from the mountainous meadows. In Marullo & Mound Eds., *Thrips and tospoviruses* (pp. 295-313). Australian National Insect Collection, Canberra.
- Vasiliu-Oromulu, L., Bărbuceanu, D. (2008). Thrips species resistent to urban pollution (Insecta: Thysanoptera). In M. Onete (ed), Species monitoring in the central parks of Bucharest (pp.92-105), Edit. Ars Docendi, Universitatea din Bucureşti.
- Vasiliu-Oromulu, L., Jenser, G., Bărbuceanu, D. (2008). Frankliniella intonsa (Trybom, 1895) a very sensitiv bioindicator for air pollution. Acta Phytopatologica et Entomologica Hungarica, 43 (1), 401-408.