246 The Southwestern Naturalist vol. 49, no. 2

mine age, but our study was limited to stems ≤ 1 m in height. Bud scars will be less evident on stems taller than 1 m.

We conclude that bud scar counting is a reliable method to estimate stem age of post oaks and blackjack oaks if an error of 2 years is acceptable. Bud scar counts would not be suitable for studies that require the exact year of stem emergence. Age determination from bud scar counts, coupled with tree coring of larger trees, would be adequate to determine age structure of oaks for most studies.

Partial funding for this study was received from the United States Army Research and Development Center, Environmental Laboratory, Vicksburg, Mississippi. We are grateful to The Wilderness Society for their support through the Gloria Barron Scholarship and to the Environmental Institute at Oklahoma State University for their support through the Presidential Fellowship program. Personnel at The Nature Conservancy, Tulsa office and the United States Army Corps of Engineers, Keystone Office provided use of equipment and allowed access to the study site. This manuscript was approved for publication by the Director, Oklahoma Agricultural Experiment Station.

LITERATURE CITED

- ABRAMS, M. D., AND G. J. NOWACKI. 1992. Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. Bulletin of the Torrey Botanical Club 119: 19–28.
- Bonkoungou, G. J. E., D. J. Raynal, and J. W. Geis. 1983. Tree population dynamics in relation to climate and forest history in the Oswegatchie Plains, northern New York. Vegetatio 54:37–59.

- CLARK, S. L. 2003. Stand dynamics of an old-growth forest in the Cross Timbers of Oklahoma. Unpublished Ph.D. dissertation, Oklahoma State University, Stillwater.
- CLARK, S. L., AND S. W. HALLGREN. 2003. Dynamics of oak (*Quercus marilandica* and *Q. stellata*) reproduction in an old-growth Cross Timbers forest. Southeastern Naturalist 4:559–574.
- CROW, T. R., W. C. JOHNSON, AND C. S. ADKISSON. 1994. Fire and recruitment of *Quercus* in a postagricultural field. American Midland Naturalist 131:84–97.
- GASSON, P. 1987. Growth rings in the aerial and root xylem of some North American temperate hardwoods. In: Ward, R. G. W., editor. Applications of tree-ring studies: current research in dendrochronology and related subjects. British Archaeological Reports, Oxford, United Kingdom. Pp. 1–19.
- HARCOMBE, P. A., C. J. BILL, M. FULTON, J. S. GLITZ-ENSTEIN, P. L. MARKS, AND I. S. ELSIK. 2002. Stand dynamics over 18 years in a southern mixed hardwood forest, Texas, USA. Journal of Ecology 90: 947–957.
- HETT, J. M. 1971. A dynamic analysis of age in sugar maple reproduction. Ecology 52:1071–1074.
- HETT, J. M., AND O. L. LOUCKS. 1976. Age structure models of balsam fir and eastern hemlock. Journal of Ecology 64:1029–1044.
- JOHNSON, P. S., S. R. SHIFLEY, AND R. ROGERS. 2002. The ecology and silviculture of oaks. CABI Publishing, New York.
- Merz, R. W., and S. G. Boyce. 1956. Age of oak seedlings. Journal of Forestry 54:774–775.
- Schweingruber, F. H. 1993. Tree and wood in dendrochronology. Springer-Verlag, Berlin, Germany.

Submitted 1 April 2003. Accepted 22 August 2003. Associate Editor was Chris Lauver.

IMMEDIATE EFFECTS OF FIRE ON THE INVASIVE ARGENTINE ANT, $LINEPITHEMA\ HUMILE$

NATHAN J. SANDERS*

Department of Biological Sciences, 371 Serra Mall, Stanford University, Stanford, CA 94305-5020
Present address: Department of Ecology and Evolutionary Biology, 569 Dabney Hall, University of Tennessee,
Knoxville, TN 37996

*Correspondent: nsanders@utk.edu

ABSTRACT—To examine how fire affects the invasive Argentine ant, *Linepithema humile*, I used pitfall traps to estimate worker abundance immediately prior to and for approximately 3 months

after a controlled burn in a northern California grassland. I found that *L. humile* abundance per trap was, on average, 75% lower after the fire than before the fire.

RESUMEN—Para examinar cómo el fuego afecta a la hormiga invasora, *Linepithema humile*, utilicé trampas de hoyos para estimar la abundancia de las obreras inmediatamente antes y durante aproximadamente tres meses después de una quema controlada en un prado del norte de California. Encontré que la abundancia de *L. humile* por trampa era, en promedio, el 75% más baja después del fuego que antes del fuego.

Invasive species threaten native ecosystems throughout the world (Vitousek et al., 1996; Mack et al., 2000). One particularly problematic species is the Argentine ant, *Linepithema humile*. Argentine ants are one of the most widespread invasive ants, and they threaten the persistence of native ant populations in many locations throughout the world (Ward, 1987; Human and Gordon, 1997; Holway, 1998*b*; Suarez et al., 1998; Sanders et al., 2001; Sanders et al., 2003). As for many other invasive pest species, controlling the spread and effects of Argentine ants is an important task in preserving native populations.

Fire, like invasive species, can alter the composition of ant communities, and there are some data on its immediate effects on ant communities. Fire can lead to increased abundance and species richness (O'Dowd and Gill, 1984) or increased richness but decreased abundance (Andersen and Yen, 1985). Fire also can lead to decreased richness and abundance (Springett, 1976); an initial decrease in abundance followed by an increase in abundance for some species, but just the opposite for others (Punttila et al., 1994); and near elimination of ants (Punttila and Haila, 1996). Thus, conclusions on the immediate effects of fire on ant communities are equivocal, perhaps because there can be both direct and indirect effects of fire on ant communities. For example, different species might be afforded different levels of protection because of their nesting behavior; those species that nest near the soil surface are more likely to suffer because of fire. Fire also might alter competitive dynamics among ant species by altering resource availability and the densities of other species.

Each May and September since 1993, a Stanford graduate student (K. G. Human, 1993–1996; N. J. Sanders, 1996–2000; N. E. Heller, 2000 to present) has documented the distribution and spread of Argentine ants at Jasper Ridge Biological Preserve (JRBP) in northern

California. Argentine ants are invading from the edges of JRBP (Human et al., 1998) and dominate communities such that native ant species richness is reduced to zero at many sites (Human and Gordon, 1997; Sanders et al., 2001). Importantly for this study, Argentine ants, unlike many native species at JRBP, nest near the soil surface.

Some Australian communities are dominated by Iridomyrmex and Monomorium, much like Argentine ants dominate communities where they invade (Andersen and Patel, 1994; Andersen, 1997). Interestingly, Andersen and Yen (1985) showed that when sites dominated by Iridomyrmex and Monomorium were burned, the richness of subordinate ant species increased, and the abundance of *Iridomyrmex* and *Mono*morium decreased. This might be because Iridomyrmex and Monomorium devote more of their workforce to foraging than do other species, which might have made them more susceptible to being burned in the fire. Similarly, I hypothesized that if a site dominated by Argentine ants was burned, the abundance of Argentine ants would decrease. Thus, fire might be a useful tool in managing the spread and impact of this important invasive species. I tested this hypothesis in 1999, when a controlled burn took place at JRBP.

JRBP is a 481-ha reserve in San Mateo County, California. The burn site was a 0.8-ha grassland within JRBP. Prior to the burn, the vegetation at the burn site consisted primarily of star thistle (*Centaurea solstitialis*), nonnative bunch grass (*Phalaris aquatica*), nonnative annual grasses, and *Baccharis pilularis* shrubs.

I used pitfall traps to sample ants before and after the burn. Pitfall traps provide a good estimate of the ground-foraging species present in a community (Bestelmeyer et al., 2000). Pitfall traps were 50-mL (2.5-cm diameter) centrifuge tubes, partially filled with a 1:1 mixture of Sierra brand antifreeze (propylene glycol) and water. I placed 33 pitfall traps at the site.

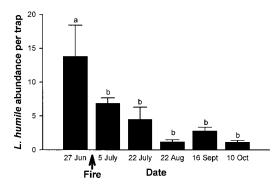


FIG. 1—Effect of fire and sampling date on Argentine ant abundance in northern California. Bars $(\pm SE)$ represent the mean number of Argentine ants per pitfall trap on all sampling dates. Bars with different letters above them are statistically different from each other as indicated by the Student-Newman-Keuls post hoc test.

Twenty-five of the traps were arranged in a 5 \times 5 grid with 5-m spacing. The remaining 8 traps were placed approximately 20 m east of the 5 \times 5 grid and were arranged in 1 row of 5, with 5-m spacing, and 1 row of 3, with 5-m spacing. I collected the pitfall traps after 72 hours. All traps were at least 10 m from the edge of the burn site. This arrangement of pitfall traps and sampling effort allowed me to sample the burn site adequately, while reducing the potentially confounding effect of sampling too near the edge of the burn, where ants from outside the site might be foraging.

I first sampled the ants at the site from 24 to 27 June 1999, and the burn took place on 28 June 1999. I then sampled the ants after the burn from 3 to 5 July. I continued to sample the site approximately every 3 weeks until mid October (total of 5 samples). During this time, Argentine ant activity usually increases at JRBP (Sanders et al., 2001). Therefore, if the fire did not affect Argentine ants, I should see an in-

crease in the number of ants in pitfall traps at the burn site.

To determine statistically the effect of fire on Argentine ant abundance, I compared the average numbers of Argentine ant workers in pitfall traps across the 5 sampling periods using an ANOVA. For the analysis, I treated each trap as a replicate, as other studies have done (e.g., Christian, 2001). Though there are obvious statistical limitations to treating each trap as a replicate, it was impossible to have multiple burned sites within JRBP so that the site could be replicated. I used the Student-Newman-Keuls (SNK) test to examine (a posteriori) the differences among pairs of sampling periods.

I collected 1,073 workers from 4 species in the pitfall traps. All but 8 (<1%) of these workers were Argentine ants; these 8 were 2 *Leptothorax nevadensis*, 1 *Solenopsis molesta*, and 5 *Hypoponera opacior*.

The fire affected Argentine ant abundance at the site (Fig. 1, Table 1). Prior to the fire, there were approximately 14 Argentine ant workers in each of the pitfall traps. Immediately after the fire, there were half as many. By October, there was an average of 1 Argentine ant worker per trap at the site. The SNK test indicated that the abundance of Argentine ants in pitfall traps prior to the fire was significantly different from the abundances on each sampling date after the fire (Fig. 1), but sampling dates after the fire were not statistically different from one another.

The controlled burn reduced the abundance of Argentine ants at the site. At least 4 mechanisms, both direct and indirect, could lead to the decline of Argentine ants after a burn. First, Argentine ant colonies nest near the soil surface, so their colonies, unlike colonies of native species (Hölldobler and Wilson, 1990), could be susceptible to the extreme

Table 1—Effect of fire on Argentine ant abundance in northern California. The response variable is abundance of Argentine ants in pitfall traps.

Source of variation	SS	df	MS	F	P
Sampling date	4,043.13	5	808.63	5.48	< 0.0001
Residual	30,076.8	204	147.44		
Total	34,119.93	209			

heat from a fire. Second, Argentine ant colonies might devote a large proportion of their colony workforce to foraging (Sanders, pers. obser.). If that is the case, then many workers could have been active outside the nest and killed by the fire. Third, the effects of fire could occur indirectly by inducing changes in habitat structure and availability of resources (Brian, 1955; Andersen, 1988; Andersen, 1991). If resources that Argentine ants rely on, such as homopterans, were dramatically reduced, then colonies might have emigrated from the burn site to suitable habitats nearby. Fourth, the fire might have reduced available moisture, which Argentine ant colonies require (Holway, 1998a; Human et al., 1998; Holway et al., 2002). If soil moisture was reduced, Argentine ant colonies might have emigrated from the site, and immigration into the site might have been reduced.

The reduction in Argentine ant abundance was caused by the fire and not by seasonal effects. On average, Argentine ant activity increases from January to September at JRBP (Sanders et al., 2001). We have detected Argentine ants at more sites in the JRBP-wide September surveys than in the January or May surveys because Argentine ant colonies are more active during the summer months, when temperatures are high. Even though Argentine ant activity should be higher in the late summer and early fall than in the early summer, I detected little activity at the burn site; this is strong evidence suggesting that the controlled burn, and not seasonal effects (Sanders et al., 2001) at this site reduced Argentine ant abundance.

This study focused on the short-term effects of fire on sites dominated by Argentine ants. The long-term effects are more important. It might be that the competitive balance between Argentine ants and native ants can be altered by prescribed burns. For example, immediately following a fire, it could be beneficial to stock native ant species, such as Prenolepis imparis and Messor andrei, at burned sites. The long-term studies at JRBP suggest that these 2 species might slow or even deter the spread of Argentine ants at this site (Sanders et al., 2001). If the spread and subsequent impact of Argentine ants can be reduced, then it might be possible to salvage lost ant biodiversity at sites invaded by Argentine ants.

I thank A. Corl for all of his help with the pitfall traps, B. Robinowitz for her help with ants, and N. Chiarello and P. Cohen for their help at JRBP. Comments by A. Classen, B. Kerr, and C. Knight greatly improved the text.

LITERATURE CITED

- Andersen, A. N. 1988. Immediate and longer term effects of fire on seed predation by ants in scler-ophyllous vegetation in southeastern Australia. Australian Journal of Ecology 13:285–293.
- Andersen, A. N. 1991. Responses of ground-foraging ant communities to three experimental fire regimes in a savanna forest of tropical Australia. Biotropica 23:575–585.
- Andersen, A. N. 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. Journal of Biogeography 24:433–460.
- Andersen, A. N., and A. D. Patel. 1994. Meat ants as dominant members of Australian communities: an experimental test of their influence on the foraging success and forager abundance of other species. Oecologia 98:15–24.
- Andersen, A. N., and A. L. Yen. 1985. Immediate effects of fire on ants in the semi-arid mallee region of north-western Victoria. Australian Journal of Ecology 10:25–30.
- Bestelmeyer, B. T., D. Agosti, L. E. Alonso, C. R. F. Brandão, W. L. Brown, Jr., J. H. C. Delabie, and R. Silvestre. 2000. Field techniques for the study of ground-dwelling ants: an overview, description, and evaluation. In: Agosti, D., J. D. Majer, L. E. Alonso, and T. R. Schultz, editors. Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, D.C. Pp. 122–144.
- BRIAN, M. V. 1955. Food collection by a Scottish ant community. Journal of Animal Ecology 24:336– 351.
- Christian, C. E. 2001. Consequences of a biological invasion reveal the importance of mutualism for plant communities. Nature 413:635–639.
- Cole, F. R., A. C. Medeiros, L. L. Loope, and W. W. Zuehlke. 1992. Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. Ecology 73:1313–1322.
- HÖLLDOBLER, B., AND E. O. WILSON. 1990. The ants. Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- HOLWAY, D. A. 1998a. Factors governing rate of invasion: a natural experiment using Argentine ants. Oecologia 115:206–212.
- HOLWAY, D. A. 1998b. Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. Oecologia 116: 252–258.

- HOLWAY, D. A., A. V. SUAREZ, AND T. J. CASE. 2002. Role of abiotic factors in governing susceptibility to invasion: a test with Argentine ants. Ecology 83:1610–1619.
- HUMAN, K. G., AND D. M. GORDON. 1997. Effects of Argentine ants on invertebrate diversity in northern California. Conservation Biology 11:1242– 1948
- HUMAN, K. G., S. WEISS, A. WEISS, B. SANDLER, AND D. M. GORDON. 1998. The effect of abiotic factors on the local distribution of the invasive Argentine ant (*Linepithema humile*) and native ant species. Environmental Entomology 27:822–833.
- MACK, R. N., D. SIMBERLOFF, W. M. LONSDALE, H. EVANS, M. CLOUT, AND F. A. BAZZAZ. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10: 689–710.
- O'DOWD, D. J., AND A. M. GILL. 1984. Predator satiation and site alteration following fire: mass reproduction of alpine ash (*Eucalyptus delegatensis*) in southeastern Australia. Ecology 65:1052–1066.
- PUNTTILA, P., AND Y. HAILA. 1996. Colonisation of a burned forest by ants in the southern Finnish boreal forest. Silva Fennica 30:421–435.
- Punttila, P., S. Koponen, and M. Saaristo. 1994. Colonisation of a burned mountain-birch forest by ants (Hymenoptera, Formicidae) in subarctic Finland. Memorabilia Zoologica 48:193–206.

- SANDERS, N. J., K. E. BARTON, AND D. M. GORDON. 2001. Long-term dynamics of the invasive Argentine ant, *Linepithema humile*, and native taxa in northern California. Oecologia 127:123–130.
- SANDERS, N. J., N. J. GOTELLI, N. E. HELLER, AND D. M. GORDON. 2003. Community disassembly by an invasive species. Proceedings of the National Academy of Sciences 100:2474–2477.
- SPRINGETT, J. A. 1976. The effect of prescribed burning on the soil fauna and on litter decomposition in western Australian forests. Australian Journal of Ecology 1:77–82.
- SUAREZ, A. V., D. T. BOLGER, AND T. J. CASE. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology 79:2041–2056.
- VITOUSEK, P. M., C. M. D'ANTONIO, L. L. LOOPE, AND R. WESTBROOKS. 1996. Biological invasions as global environmental change. American Scientist 84:468–478.
- WARD, P. S. 1987. Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the lower Sacramento Valley and its effects on the indigenous ant fauna. Hilgardia 55: 1–16.

Submitted 25 February 2003. Accepted 18 September 2003. Associate Editor was Steven Goldsmith.

CRAYFISHES OF OKLAHOMA REVISITED: NEW STATE RECORDS AND CHECKLIST OF SPECIES

CHRISTOPHER A. TAYLOR,* SHANE N. JONES, AND ELIZABETH A. BERGEY

Center for Biodiversity, Illinois Natural History Survey, 607 East Peabody Drive, Champaign, IL 61820 (CAT)
Oklahoma Biological Survey and Department of Zoology, 111 East Chesapeake Street, University of Oklahoma,
Norman, OK 73019 (SNI, EAB)

*Correspondent: ctaylor@mail.inhs.uiuc.edu

ABSTRACT—Examination of museum records and field observations have included 4 new records for species of crayfish in Oklahoma (*Cambarellus puer, Orconectes deanae, O. lancifer,* and *O. macrus*) and a new drainage record for *O. neglectus neglectus*. These records bring the number of crayfish known in Oklahoma to 28 and emphasize the importance of revisiting aquatic habitats in regions that have been visited previously. Such records can help in determining the conservation status of poorly known taxonomic groups.

RESUMEN—La revisión de registros de museos y observaciones de campo mostró 4 registros nuevos de especies del cangrejo de río en Oklahoma (*Cambarellus puer, Orconectes deanae, O. lancifer* y *O. macrus*) y un nuevo registro de cuenca para *O. neglectus neglectus*. Estos registros suben el número total de cangrejos de río conocidos en Oklahoma a 28 y destacan la importancia de visitar nuevamente hábitats acuáticos en regiones que se han visitado previamente. Tales registros pueden ayudar en la determinación del estado de conservación de grupos taxonómicos poco conocidos.