firm, cohesive soil. It was soft and easily removable. It was free from any pebbles and was similar to the loose plow soil.

The observation of the easily distinguishable loose fill material devoid of any pebbles clearly suggested that the fissures had once been open and later filled up from the top with loose soil. Thus, it may be possible to distinguish earthquake-generated fissures by examining the nature of the filled material. Also, the presence of organic material in the filled material can be used to get a minimum age for the earthquake. A cursory search for organic material (pieces of wood, grass, leaves, shells, etc.) within the fill material was unsuccessful.

Figure 3 is a schematic diagram showing a conceptual view of how the fissures associated with the 1967 Koyna earthquake would compare with those for a prehistoric earthquake. The fissures for a prehistoric earthquake would be buried beneath recent sedimentary deposits.

Thus, by identifying paleo fissures in road cuts and other exposures evidence can be sought for prehistoric earthquakes. C-14 dating of trapped organic material in these fissures can be used to possibly determine the dates of prehistoric earthquakes (Figure 3).

Conclusions

From an examination of the features in the trench near Kadoli we conclude that:

1. Fissures formed during ground shaking during a large

earthquake are preserved in a sedimentary column.

- 2. The fissures encountered in the trench near Kadoli were associated with the 1967 earthquake. This conclusion is in concordance with the location and description in the GSI report and eyewitness accounts.
- 3. These fissures could be traced to at least 2 m below the surface to the rocks below.
- 4. The fill material in the fissures was distinctly different from the host material and can be used to identify other fissures formed by earthquakes and hence used to search for prehistoric earthquakes.
- 5. The date of the earthquake can be obtained by dating any organic remains within the fill material using ¹⁴C method or by other techniques.
- 1 Gupta, H. K., in Reservoir-Induced Earthquakes, Elsevier, Amsterdam, 1992, pp. 33-86
- 2. Sathe, R. V., Phadke A. V., Peshwa V. V. and Sukhatankar R. K., J. Univ. Poona. Science and Technology Section, 1968, 34, 15-19.
- 3. Officers of the Geological Survey of India, in A Geological Report on the Koyna Earthquake of 11th December, 1967, Satara District, Maharashtra State, Geological Society of India, 1968, p. 242.

ACKNOWLEDGEMENTS. The trenching operation was possible only due to the timely help and efforts of Mr S. Bhingare, Superintending Engineer, Koyna Project. Our sincere thanks to him and to Dr Sahasrabudhe, who was kind enough to share his keen insight based on his vast experience of working in the Koyna area. We are most grateful to him for his help and guidance. We also want to thank Drs. Kulkarni and Tandale for helpful discussions.

Received 5 November 1994; accepted 22 December 1994

Tree water relations along the vegetational gradient in the Himalayas

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Natural vegetation of the central Himalayas reflects a strong, extensive environmental gradient. The importance of environment, in particular drought, in controlling species distribution and performance is poorly understood. Indirect evidence and a few measurements, however, suggest that tree distribution is strongly related to drought. A study of water relations of trees in native forests along the environmental gradient up the face of the outer Himalayas near Nainital should make clear the role of water in controlling forest properties, and help test generalizations about tree water relations that were developed in other climates.

Trees in the Himalayas are subject to drought for several months each year. Study of their response to drought

can contribute to the understanding of the local patterns of species distribution and performance, as well as to plant water relations in general. Data about water relations are available for many taxa related to species in the Himalayas; this information, however, may not be useful in the Himalayas, where trees grow with a different seasonality of rainfall, and many have different leaf and wood properties compared to related species elsewhere. A study of the responses of Himalayan trees to drought will provide a critical test of generalities developed in other climates. Many aspects of ecology of some Himalayan trees are already well known, allowing the significance of their water relations characteristics to be interpreted effectively.

Vegetation-environment relationships

Ecologists study the control of plant distribution by relating the vegetational changes along environmental gradients to associated changes in the environment. The Himalayas present, perhaps, the premier vegetational gradient on the Earth, ranging from tropical forests at the base to alpine meadows within a map distance of

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100-200 km. A primary determinant of vegetational change is the temperature, but soil properties and water availability too, among other factors, modify vegetation within limits permitted by the temperature regime. Although few environmental factors have been studied in detail in the Himalayas, the long dry season inherent in the monsoon climate, with most rainfall during only 3 months, suggests that water may become limiting on many sites during the other 9 months.

In other parts of the world with a dry season, plant water relations provide a cornerstone for interpreting vegetational and plant distributions across environmental gradients (e.g. the Pacific Northwest of the United States^{1,2}). Ecologists in Kumaun, in the central Himalayas, have studied vegetation patterns, ecosystem dynamics, timing of plant processes and plant-nutrient relationships in substantial detail^{3,4}. But there have been only few measurements of water relations in the Himalayas, especially for trees in natural forest. The following fundamental, critical questions about the response of Himalayan vegetation to variation in water availability remain unanswered:

- 1. Does the dry period in the Himalayas produce moisture stress in trees, or is the drying of soil not deep enough to encompass the rooting zone, at a time of the year when trees are insensitive to drought, or not severe enough to modify the distribution and functioning of trees?
- 2. If moisture stress develops in trees, when does it occur, how intense is it, and which plant processes does it affect?
- 3. If severe moisture stress does interfere with tree survival or growth, what differences in its impact exist among vegetation types, among sites within a vegetation type, and among species within a site, for example, species that differ in their leaf properties?

Water relations in Himalayan vegetation

Studies in the central Himalayas indicate indirectly that moisture stress can be severe, and that stress varies among communities, sites and species:

- 1. Tree diameter decreased during the dry season in all the species studied, more so in shrubs than in trees, and more so in deciduous than in evergreen species; water loss from outer tissues, associated with a seasonal moisture deficit, causes such a shrinkage of tree trunks.

 2. Tree diameter growth of subalpine conifers, just east of Kurraug in North varied with receiving the seasonal state.
- 2. Tree diameter growth of subalpine conifers, just east of Kumaun in Nepal, varied with precipitation of the year when growth occurred, and of the previous year, strongly suggesting control of tree growth by water availability.
- 3. Forest diversity, cover and species composition changed across a gradient of soil moisture measured in November, the driest month⁸.

- 4. Germination of tree seeds varied among species in its sensitivity to moisture availability, although not to temperature. The species most sensitive to limited water had the smallest natural ranges^{4, 9, 10}.
- 5. Tree species differed in seedling growth response to drought when grown in culture^{9, 10}. Species whose seedlings were least affected by experimentally imposed drought grew on drier sites than species more affected by drought.
- 6. During pre-monsoon drought, leaves of broad-leaf trees often wilted. In 1991, needles of pines, which started to elongate in April, did not reach full size until after monsoon rains began (D. B. Zobel, unpublished data).

Water relations measurements

Although these observations and experiments suggest that moisture stress in Himalayan trees can be severe and that it affects their growth and distribution, direct measurement of plant water status in the field is required to confirm such hypotheses. Measurements of soil moisture and extrapolation from experimental studies cannot replace measurements of trees in natural forests. Plant water status is assessed as plant water potential11, which is measured most effectively using a pressure chamber". The water potential is usually assessed at two times of the day: (i) early morning, when the water potential of trees is most favourable (and should be near equilibrium with that of the soil), and (ii) mid-day, when water stress will be most severe. Few water potential measurements have been made for natural Himalayan trees: these few, however, indicate that water potentials do become low enough to interfere with plant processes, and perhaps to kill trees, both in mid-winter and during hot weather before the monsoon¹³ (see also D. B. Zobel, unpublished data). Although water potentials were most severe in winter¹³, whether the dormant trees react adversely to them is uncertain. Minimum water potentials before the monsoon, while less severe13, were low enough to interfere with physiological processes in most trees. Pre-monsoon stress seems likely to disrupt plant growth; during that period, the dominant evergreens of the Himalayas are expanding new leaves 14.15, which will provide most of the photosynthate for the following year. A favourable water status allows the development of turgor pressure, the force that expands cells in the developing leaves. If water potentials measured during leaf enlargement are low, an additional aspect of water relations requires study: Is the water limited enough to prevent the development of the level of turgor required for leaf expansion?

Direct measurement of turgor pressure in the field is impossible for tree leaves, but one can estimate turgor based on a combination of field water potential and

laboratory measurements made on leaves collected from the field. Plant water potential includes two components - pressure potential (equal to turgor pressure) and osmotic potential; together they comprise the water potentialosmotic potential + pressure potential = water potential. Osmotic potential, always less than zero, is related to the concentration of cell solutes, a characteristic over which some plants exert substantial control, and which often changes with season⁶. If water potential remains the same while the concentration of cell solutes increases, driving the osmotic potential farther below zero, the pressure potential will increase. Osmotic potential can be estimated in the laboratory by analysis of pressurevolume curves developed for twigs collected from the field¹². Using pressure-volume curves, one can also estimate the pressure potential that would be associated with water potentials measured in the field.

Plants also differ in their leaf cell wall elasticity, which may affect the pressure potential. Pressure potential of plants with elastic cell walls will decline slower as the plants lose water than for plants with less elastic walls¹². Tissue elasticity can also be measured from pressure-volume curves.

Plants also control their water status by regulating the size of stomatal openings, which modify the rate of water loss; reducing water loss can reduce the effect of limited soil moisture on water potential. Using a diffusion porometer¹⁶, the water vapour conductance of the leaf surface (controlled by the degree of stomatal opening) can be measured in the field at the same time as the water potential.

Differences in the conductance of water by xylem also contribute to differences in species water relations^{17, 18}, and may compensate for or magnify the differences measured at the leaf level.

Interpreting water relations parameters

In some cases, the components of water potential, tissue elasticity, stomatal behaviour and xylem conductivity correlate well with the observed distribution and importance of plants in the field ¹⁹⁻²¹. In other cases, however, water relations attributes correlate poorly with plant distribution ^{22,23}: apparently, water is not a critical factor modifying vegetational composition in those areas, or its effect is through a mechanism not measured by these methods.

Complicating the correlations between plant distribution and water relations measurements is the complex interrelationship of plant behaviour to ecological success^{11,24}. There are several effective strategies for a plant faced with limited water. A plant characteristic required by one strategy may be unfavourable in alternative strategies. One cannot judge the fitness of a plant for drought based on a single characteristic, but only

by studying several characteristics contributing to its possible strategies. Further complicating the interpretation is that an effective strategy in one environment may be inappropriate in a different environment. As an example, keeping stomata open as drought intensifies allows a plant to continue photosynthesis and provide more dry matter for eventual use in growth; an alternative behaviour is to close the stomata at the first sign of drought, reducing the water loss but losing the opportunity for dry weight gain. The former behaviour is suitable where droughts do not become too severe; the latter is required for severe drought but leaves the plant at a disadvantage where drought is predictably mild. Thus, one can interpret water relations data effectively only by understanding a suite of characteristics for a group of species that compete with each other, along with details about their other adaptive behaviours and their environment.

A study in progress

Scientists from Kumaun University, Nainital, and from Oregon State University, USA, have begun a cooperative project to measure water relations of Himalayan trees - 'The timing of drought: Effects on water relations of Himalayan tree species' - approved by the Department of Science and Technology, New Delhi, and funded by the US National Science Foundation. Field water potentials and leaf conductance for water vapour will be measured around the year in four major types of vegetation along the environmental gradient in the outer Himalayas near Nainital: sal (Shorea robusta), chir pine (Pinus roxburghii), banj oak (Quercus leucotrichophora), tilonj oak (Q. floribunda), and in an important rare type in Nainital, cypress (Cupressus torulosa). In addition, species comparisons will be made among the different dominant species where they grow together, to look for species differences in a common environment. Further comparisons will be made between the dominant evergreen species and the deciduous species that grow with them but are much less important, to determine to what extent differences in water relations contribute to evergreen dominance. Samples collected from the field will be subjected to pressure-volume analysis in the laboratory, to estimate tissue elasticity and osmotic and pressure potentials for the field sampling days. Measurements in the field will cover two years at all sites, while pressure-volume analysis for each sample species will be made several times during a year. Differences in xylem conductance will also be assessed for twigs of each species. The data will be used to test hypotheses such as:

1. Water potentials become low enough to determine the distribution of Himalayan trees and vary among forest types, with lowest potentials during winter at high elevations and during the pre-monsoon heat at low elevations.

- 2. Trees subject to low water potentials during leaf growth reduce the osmotic potentials and increase the leaf elasticity during that period; trees without water stress before the monsoon adjust their leaf properties much less.
- 3. Evergreen dominant trees, compared to co-occurring deciduous species, adjust their leaf properties (osmotic potential, elasticity, conductance) more as season and water availability change.

Himalayan data will also provide a valuable test of generalities about water relations of temperate-climate trees, most of which^{25, 26} were developed in areas with seasonality different from the monsoon climate, i.e. with no predictable dry season or with drought in June-August. We anticipate, for example, that there will be differences between water relations of trees that expand leaves during drought and then encounter monsoon rainfall in the Himalayas, and of trees that expand leaves in the wet season and then encounter drought during most of their growing season, as in the coastal western United States. Our data will also contribute to the understanding of the control of species' distributions, a topic recently emphasized out of the concern for the effects of (apparent) global climatic changes. If, for example, yearto-year fluctuations of monsoon rainfall increase, making dry years even drier, what might be the effects on Himalayan trees?

- 1. Waring, R. H. and Schlesinger, W. H., Forest Ecosystems. Concepts and Management, Academic Press, Orlando, 1985.
- 2. Zobel, D. B., McKee, W. A., Hawk, G. M. and Dymess, C. T., Ecol. Monogr., 1976, 46, 135-156.
- 3. Singh, J. S. and Singh, S. P., Bot. Rev., 1987, 53, 80-192.
- 4. Singh, J. S. and Singh, S. P., Forests of Himalaya, Gyanodaya Prakashan, Nainital, 1992.
- 5. Singh, S. P., Ralhan, P. K., Upadhyay, V. P. and Negi, G. C. S., J. Vegetation Sci., 1990, 1, 165-172.
- 6. Kozlowski, T. T., Kramer, P. J. and Pallardy, S. G., The Physiological Ecology of Woody Plants, Academic Press, San Diego, 1991.
- 7. Suzuki, E., Bot. Mag. (Tokyo), 1990, 103, 297-312.
- 8. Rikhari, H. C., Chandra, R. and Singh, S. P., Proc. Indian Nat. Acad. Sci., 1989, B55, 421-438.
- 9. Rao, P. B. and Singh, S. P., Ann. Bot., 1985, 56, 783-794.
- 10. Rao, P. B., Ann. Bot., 1988, 61, 531-540.
- 11. Kramer, P. J., Water Relations of Plants, Academic Press, New York, 1983.
- 12. Pallardy, S. D., Pereira, J. S. and Parker, W. C., in *Techniques and Approaches in Forest Tree Physiology* (eds. Lassoie, J. P. and Hinckley, T. M.), CRC Press, Boca Raton, 1991, pp. 27-76.
- 13. Dhaila, S., Ph D Thesis, Kumaun University, Nainital, 1991.
- 14. Ralhan, P. K., Khanna, R. K., Singh, S. P. and Singh, J. S., Vegeiauo, 1985, 60, 91-101.
- 15. Negi, G. C. S. and Singh, S. P., Int. J. Biometeorol., 1992, 36, 233-242
- 16. Smith, W. K. and Hollinger, D. Y., in Techniques and Approaches in Forest Tree Physiology (eds., Lussoie, J. P., and Hinckley, T. M.), CRC Press, Boca Raton, 1991, pp. 141-174.

- 17. Tyree, M. T. and Sperry, J. S., Annu Rev. Plant Phys. Mol. Biol., 1989, 40, 19-38.
- 18 Ewers, F. W. and Cruiziat, P., in Techniques and Approaches in Forest Tree Physiology (eds Lassoie, J. P. and Hinckley, T. M.), CRC Press, Boca Raton, 1991, pp. 91-115.
- 19. Abrams, M. D., Tree Physiol., 1990, 7, 227-238.
- 20. Cochard, H., Tree Physiol., 1992, 11, 73-83.
- 21. Anderson, D. J., Stricker, P., Williams, S. and Adam, P., Func. Ecol., 1988, 2, 391-397.
- 22. Bannister, P. and Kissel, R. M., Flora, 1986, 178, 329-342.
- 23. Abrams, M. D., Schultz, J. C. and Kleiner, K. W., For. Sci., 1990, 36, 970-981.
- 24. Ishida, A., Yamamura, Y. and Hori, Y., Ecol. Res., 1992, 7, 213-223.
- 25. Abrams, M. D., For. Sci., 1988, 34, 1030-1046.
- 26. Lassoie, J. P. and Hinckley, T. M. (eds.), Techniques and Approaches in Forest Tree Physiology, CRC Press, Boca Raton, Florida, 1991.

ACKNOWLEDGEMENTS. Research support is provided by US National Science Foundation grants INT-9312052 and INT-9404043.

Received 30 November 1994; accepted 9 December 1994

Impact of fire on a dry deciduous forest in the Bandipur National Park, southern India: Preliminary assessment and implications for management

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The effect of fire was analysed in two plots in a dry deciduous forest of Bandipur National Park, Karnataka. The less fire-prone plot had a higher tree density (HD) and included more tree and shrub species than the more fire-prone plot with lower tree density (LD). The LD had fewer and smaller thickets, whereas in the HD the presence of thickets had resulted in closure of the vegetation with more abundant weeds. Regeneration was higher in the LD, despite the greater rate of sapling mortality. Fire is shown to have impact on the tree/grass equilibrium and weed control. Our study also corroborates that protection from fire allows colonization by semievergreen trees and shrub species, while frequent fire opens up the vegetation. Fire should be used as a management tool to avoid catastrophic rare fires, to regulate weed expansion and to maintain plant communities for the sustenance of the protected fauna.

In India, fire has been used since millennia to open up the vegetation for cultivation. Until recently, slash and